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Comparison of quantitative trait loci controlling seedling characteristics at two seedling stages using rice recombinant inbred lines

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Abstract A better understanding of the genetics of seedling characteristics in rice could be helpful in improving rice varieties. Zhenshan 97 and Minghui 63, the parents of Shanyou 63, an elite hybrid developed during the last decade in China, vary greatly with respect to their physiological and morphological traits at the seedling growth stage. In this study, we used a population of 240 recombinant inbred lines derived from a cross between Zhenshan 97 and Minghui 63 to identify quantitative trait loci (QTL) for seedling characteristics. All plant material was grown in hydroponic culture. Data for the following characters were collected at 30 days and 40 days post-sowing: plant height, shoot dry matter weight (SDW), maximum root length, root dry weight (RDW), total dry weight , and root-shoot ratio (the ratio of SDW to RDW). Analysis using composite interval mapping detected 16 QTL for the six traits in 30-day-old seedlings. Of these 16 QTL, Minghui 63 alleles increased trait values at only two of them. The QTL in the vicinity of R3166 on chromosome 5 simultaneously influenced PH, SDW, MRL, RDW, and TDW in the same direction. Twenty QTL were detected for the same traits in the 40-day-old seedlings. However, at this stage Minghui 63 alleles increased trait values at eight QTL. The QTL linked to R3166 also affected PH, SDW, MRL, RDW, and TDW. Only four QTL were common to the two stages. These results clearly indicate that different genes (QTL) control the same traits during different time intervals. Zhenshan 97 alleles had positive effects during the first 30 days of seedling growth, but thereafter the positive effects of Minghui 63 alleles on seedling growth gradually became more pronounced.

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Introduction

Strong seedling vigor or rapid seedling growth is a major breeding target in rice and other crops (Karrel et al. 1993; Redoña and Mackill 1996a) as seedling vigor is closely associated with crop growth and yield (Ellis 1992). Substantial genetic variation for improvement exists in rice varieties (Redoña and Mackill 1996a), and the molecular dissection of the genetic basis of seedling characteristics could be helpful in attaining this improvement (Redoña and Mackill 1996b). Previous investigators have focused on the quantitative trait loci (QTL) mapping of seedling vigor traits in a fixed initial stage of seedling growth— normally within the first 15 days—and mapped many QTL for germination rate, shoot length, shoot weight, and coleoptile length (Redoña and Mackill 1996c; Cui et al. 2002).

Root and shoot systems affect seedling vigor, and these systems reciprocally benefit one another because of the relationship between water and nutrient absorption and carbohydrate production. The traditional statement “the more root the better” is generally accepted in agriculture. Root length, weight, and volume are reported to have medium-to-high heritabilities (Chang et al. 1982; Loresto et al. 1983) and high genetic diversity (O’Toole and Bland 1987). Thus, theoretically, root traits are very suitable to QTL mapping, although the difficulty in measuring root growth characteristics on a large scale in the field has inhibited genetic analyses. Genetic variation and QTL for root traits have been reported (Ingram et al. 1994; Champoux et al. 1995; Redoña and Mackill 1996c). QTL for root traits were initially studied in several *Oryza japonica* × *indica* inter-subspecific crosses (Champoux et al. 1995; Redoña and Mackill 1996c; Price and Tomos 1997; Yadav et al. 1997; Zheng et al. 2000) and then extended to *indica* × *indica* crosses (Ali et al. 2000; Kamoshita et al. 2002).

It is easy to measure the root length and collect all of the roots for dry-weight measurements in hydroponic culture. The well-distributed nutrient solution also minimizes the differences caused by fertilizer concentration. The overall size and maximum depth of the rice root system and individual root thickness are positively related to drought resistance in the field, whether measured in the field-grown plants or in hydroponic cultures (Yoshida and Hasegawa 1982; Loresto et al. 1983). Price et al. (1997) showed that traits such as maximum root length and adventitious root thickness of rice varieties grown hydroponically can be related to drought resistance in the field and to growth in soil. QTL have been shown to control root growth traits such as maximum root length at various stages of root development in an F_2 population (Price and Tomos 1997).

Most of the QTL mapping studies have been limited to analyzing the performance of a trait observed at a fixed time or stage of ontogenesis. From the view of developmental biology, different genes (QTL) may have different expression dynamics during development. In the last decade, molecular markers have been applied to map QTL and to estimate their effects in different developmental stages (Bradshaw and Stettler 1995; Plomion et al. 1996; Price and Tomos 1997; Verhaegen et al. 1997). Trait values (Bradshaw and Stettler 1995; Plomion et al. 1996; Price and Tomos 1997; Verhaegen et al. 1997) or trait value increments (Bradshaw and Stettler 1995; Plomion et al. 1996; Verhaegen et al. 1997; Wu et al. 1999) observed at sequential time intervals were used to estimate QTL effects. The phenotypic values of plant height and tillers per plant are easy to score throughout the growth stage of the rice plant and have been used as model traits for time-dependent QTL mapping in some related studies (Yan et al. 1998; Wu et al. 1999; Cao et al. 2001).

Zhenshan 97 and Minghui 63, the parents of Shanyou 63, an elite hybrid developed during the last decade in China, vary greatly with respect to their physiological and morphological traits at the stage of seedling growth. In the investigation reported here, we used a population of 240 recombinant inbred lines (RILs) derived from a cross between Zhenshan 97 and Minghui 63 to identify QTL for seedling characteristics. Our first objective was to dissect the genetic basis of seedling characteristics and determine the relationship between the root system and the shoot. Our second objective was to identify the gene (QTL) expression pattern by comparing QTL analyses at two different growth stages.

Materials and methods

The plant population consisted of 240 F_9 RILs (F_{10}) constructed by a single seed descendant from an elite rice hybrid cross between two *Oryza indica* cultivars, Zhenshan 97 and Minghui 63 (Xing et al. 2002). The RILs, the parents of the RILs, and the F_1 were grown hydroponically at the experimental farm of Huazhong Agricultural University in the 2001 rice-growing season in Wuhan, China. The nutrition solution for hydroponic cultures was prepared as recommended by the International Rice Research Institute (pH 5.0; Yoshida et al. 1976).

The seeds were sown on 15 June in large plastic boxes filled with sand. After 7 days growth in the sand bed, 20 seedlings from each line with good performance were selected for transplanting into wooden frames suspended in the tank of nutrient solution. The stem base of each seedling was surrounded with sponge and then anchored to the well. Every 10 days the sponge was replaced with a new one. Each wooden frame had three rows of wells and each row had five wells for a total of 15 wells per board, with 10 cm between wells within each row and 16.5 cm between rows. The volume of solution for each pool was 1,800 l. The stock nutrient solution was added every week, the nutrient was replaced every 2 weeks, and the pH was adjusted every week.

Experiments were conducted following a randomized complete block design with four replications. Five seedlings for each line were transplanted into a one-row plot. At 30 days post-sowing, the five plants for each line in two replications were individually measured to score the following traits: plant height (PH, in centimeters), maximum root length (MRL, in centimeters), shoot dry matter weight (SDW, in milligrams), root dry weight (RDW, in milligrams), total dry weight (TDW, in milligrams), and root-shoot ratio (RSR, scored as RDW divided by SDW). Plants in the remaining two replications were measured for the above traits at 40 days post-sowing. Trait measurements averaged over the two replications at the same stage were used as the raw data in the analyses.

Data analyses

Basic statistics were run using the software STATISTICA (StatSoft 1997). A genetic linkage map including 221 marker loci had been constructed in a previous study (Xing et al. 2002). Forward stepwise regression and backward elimination regression methods were used to choose significant markers for each trait. When the QTL were analyzed by composite interval mapping (Zeng 1994) using the computer program QTL CARTOGRAPHER ver. 1.15 (Basten et al. 2001), all of the significant markers were selected to control for the genetic background, and window size (10 cM) was used to control for the genetic background. Thresholds for logarithm of odds (LOD) score were estimated by permutation tests (Churchill and Doerge 1994) with 1,000 replicates. An overall (genome-wide) significance level of 0.05 was used to declare QTL.

Results and discussion

Trait performance

At 30 days post-seed sowing, Zhenshan 97 had smaller values than Minghui 63 for PH but larger values for SDW, MRL, TDW, and RSR. The differences between the parents were significant at P=0.05 (Table 1). Negative midparent heterosis was observed for SDW, MRL, RDW, TDW, and RSR, coincident with the smaller traits of Minghui 63. Also, the values of Shanyou 63 for SDW, WRL, RDW, and RSR were smaller than those of both parents, while Shanyou 63 had a slightly larger PH than the midparent value. The means of the RILs for the six traits were approximately equal to hybrid values except for PH. The six traits expressed transgressive segregation in both directions.

At 40 days post-sowing, the performance of the six traits between the parents showed the same trend as at 30 days (Table 1). Again, all six traits expressed transgressive segregation in both directions. The trait values of Shanyou 63 sharply increased during the 10 days following the 30-day post-sowing measurements. In addition, Shanyou 63 showed positive midparent heterosis and better parent heterosis for SDW, MRL, RDW, TDW,

Table 1 Trait performance of the RIL population, the hybrids, and their parents at two stages under hydroponic culture

Trait[a]	Days[b]	RIL population		Zhenshan 97	Minghui 63	Mid-parent	Shanyou 63[c]	LSD[d] (0.05)
		Mean	Range					
PH	30	36.6	25.7–46.1	37.5	42.4	40.0	41.9 (4.8)	1.7
	40	41.4	32.1–54.7	45.6	49.6	47.6	47.1 (−1.1)	1.9
SDW	30	667.6	200.0–1200.0	881.3	752.1	816.7	682.4 (−16.4)	26.0
	40	1074.6	211.7–1551.7	1148.3	931.7	1040.0	1578.3 (51.8)	51.3
MRL	30	14.8	11.1–19.2	18.1	14.9	16.5	14.7 (−10.9)	0.8
	40	36.4	30.7–43.8	36.9	31.6	34.3	37.8 (10.2)	1.1
RDW	30	72.2	16.0–120.0	109.0	81.3	95.2	76.4 (−19.7)	11.5
	40	440.8	200.0–730.0	470.0	343.3	406.7	706.7 (73.8)	30.1
TDW	30	738.2	230.0–1298.0	990.3	833.4	916.9	758.8 (−17.2)	67.7
	40	1526	840.0–2101.7	1618.3	1275.0	1446.5	2285.0 (58.0)	108.7
RSR	30	10.9	4.6–19.2	12.3	10.8	11.6	9.0 (−4.3)	1.0
	40	40.5	25.6–58.8	41.7	37.0	39.4	45.5 (15.5)	2.8

[a] PH, Plant height (cm); MRL, maximum root length (cm); SDW, shoot dry matter weight (mg); RDW, root dry weight (mg); TDW, total dry weight (mg); RSR, root-shoot ratio

[b] Number of days post-sowing at which the trait was measured

[c] Midparent heterosis in parentheses (%)

[d] Least significant difference ($P=0.05$)

and RSR. Midparent heterosis of SDW, RDW, and TDW was over 50%, while for PH, Shanyou 63 was slightly shorter than the midparent. The means of RILs for the six traits were approximately equal to the midparent values. During the period 30 days to 40 days post-sowing, the values for MRL, SDW, RDW, TDW, and RSR showed a rapid increase in the population.

We found the phenotypic values of the early-maturing parent, Zhenshan 97, to be larger than those of Minghui 63 for all of the traits tested except PH during the first 30 days and 40 days of seedling growth. However, at maturity the complete opposite has been shown (Yu et al. 1997; Xing et al. 2002). When grown under normal conditions, Minghui 63 always had much larger phenotypic values for most of the agronomic traits than Zhenshan 97.

Correlation among traits

PH had a highly significant positive phenotypic correlation with SDW (0.56), MRL (0.40), RDW (0.50) and TDW (0.57) but not with RSR (−0.11) in the first 30 days of seedling growth. SDW had the highest correlation with RDW at both stages (0.83 and 0.84). Surprisingly, SDW showed a highly significant negative correlation with RSR (−0.25) at day 30, but no significant correlation with RSR (−0.02) at day 40. RDW showed highly significant positive correlations with MRL at the two stages ($r=0.71$ at 30 days and 0.42 at 40 days).

QTL analysis

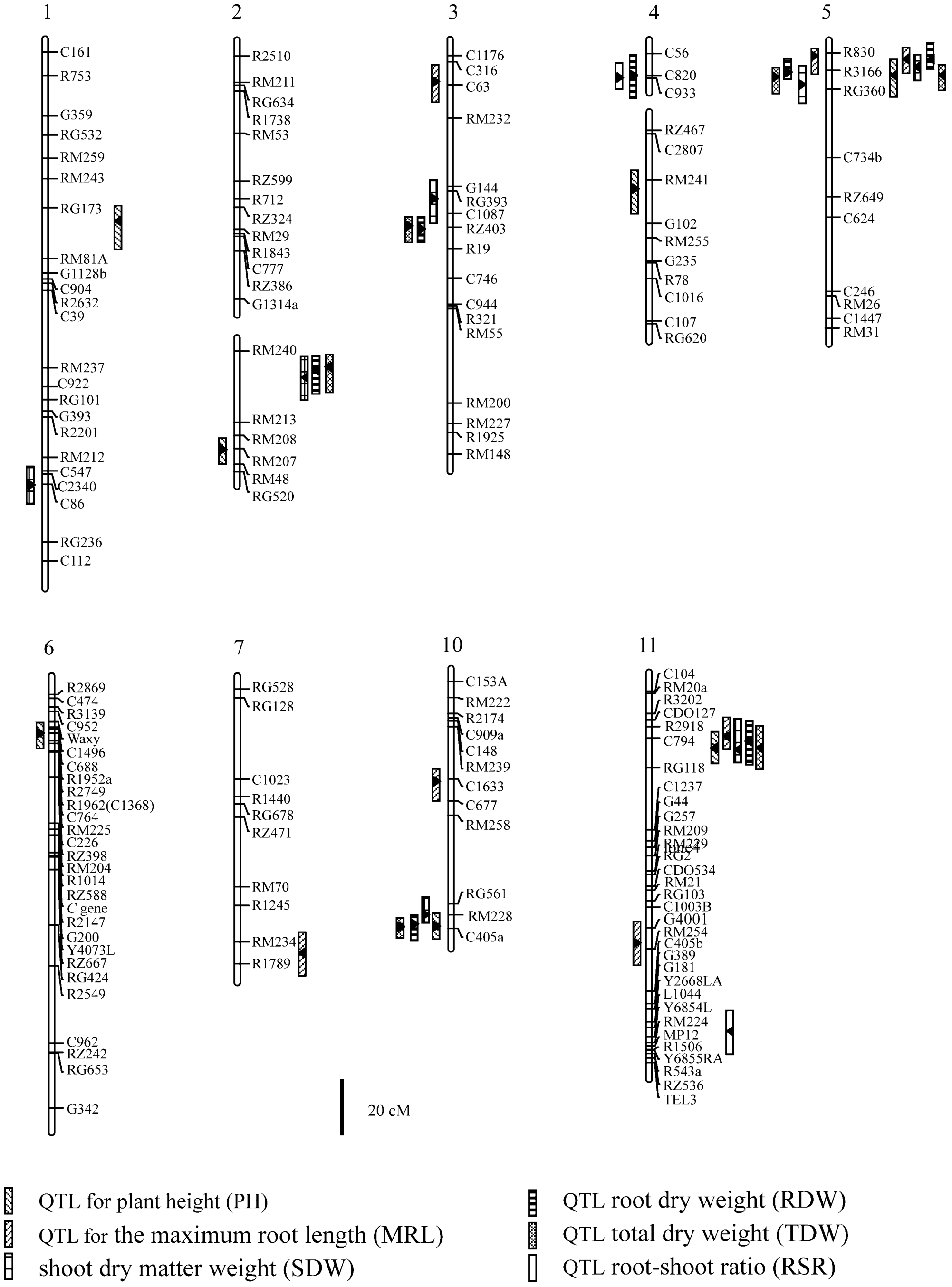
To determine a realistic threshold for declaring a QTL, we conducted 1,000 permutation tests for each of the six traits. The threshold LOD at genome-wide significance levels of 0.05 ranged between 2.6 and 2.9 for the six traits at both stages. Thus, the threshold of 2.9 was used to claim the presence of a QTL. Using composite interval mapping, we detected 16 and 20 QTL for the six traits measured at day 30 and day 40 (Table 2), respectively. Only four QTL were common to both stages (Fig. 1).

Three and four QTL affecting PH were identified at 30 days and 40 days post-sowing, respectively. There was no QTL common to both stages. The Minghui 63 alleles at the QTL on chromosomes 1 and 6 caused an increase in PH, but at the other loci they decreased PH. The total variability explained by the identified QTL was 20.7% and 23.5% at 30 days and 40 days post-sowing, respectively.

For MRL, three and four QTL were detected at 30 and 40 days post-sowing, respectively. One QTL on chromosome 5 was common to both stages. QTL on chromosomes 5, 7, and 10 showed larger effects and explained a relatively large proportion of phenotypic variance. The Zhenshan 97 genotypes at six of the seven QTL (except *qMRL3* on chromosome 3) had increasing effects on MRL. QTL identified at 30 days and 40 days post-sowing explained 19.6% and 19.8% of MRL phenotypic variance, respectively.

Three and four QTL for SDW were resolved at both stages and together accounted for 19.3% and 24.7% of phenotypic variance, respectively. A QTL on chromosome 5 was common to both stages. Zhenshan 97 alleles at five loci contributed to the increase in SDW. The QTL *qSDW5* within interval R3166–RG360 had the largest additive effect (66.3 mg SDW per seedling), accounting for 12.6% of the phenotypic variance at 30 days post-sowing. The QTL *qSDW10* had the largest effect on SDW, contributing 13.1% of the observed phenotypic variance at 40 days post-sowing.

Fig. 1 Chromosome distribution of QTL in the molecular linkage map as detected by composite interval mapping. QTL on the *right* and *left sides* of the chromosomes were detected at 30 days and 40 days post-sowing, respectively. The *bar length* represents a one-LOD support interval, and the *triangles inside the bars* indicate the positions with LOD peaks



For RDW, three and four QTL were detected at both stages and together explained 20.3% and 22.4% of phenotypic variance, respectively. One QTL on chromosome 5 was detected at both stages, and it had large effects on RDW at both stages. Zhenshan 97 alleles at four of the six QTL increased RDW.

Three QTL for TDW were identified at both 30 days and 40 days and combined to explain 21.4% and 23.6% of the phenotypic variance, respectively. One QTL on chromosome 5 was common at both stages and had comparatively large effects. Because SDW and RDW are the components of TDW, it is not surprising that all of the QTL for TDW were also detected in the same regions, or in closely linked regions, affecting SDW and RDW. Theoretically, the effect of *qTDW* should be equal to the sum of correspondent *qSDW* and *qRDW*. In fact, the additive effects of three *qTDW* QTL (−53.8, −72.6, and −45.7) were nearly equal to the sum of the corresponding *qRDW* and *qSDW* QTL (−52.1, −72.3, and −46.5) at 30 days post-sowing. At 40 days post-sowing, the additive effects of the three *qTDW* QTL were also nearly equal to the sum of corresponding *qRDW* and *qSDW* QTL.

For RSR, only one QTL was detected on chromosomes 11 and 4 at 30 days and 40 days, respectively. Minghui 63 alleles at the loci increased RSR. The location

Table 2 QTL for the six traits detected by composite interval mapping of 30-day-old seedlings and 40-day-old seedlings (LOD threshold = 2.9)

Traits	QTL[a]	Marker interval[b]	30-day-old seedlings			40-day-old seedlings		
			LOD	Additive[c]	R^2	LOD	Additive[c]	R^2
PH	*qPH1*	RG173–RM81A	5.2	1.2	9.8			
	qPH2	RM207–RM48				6.4	−0.8	7.1
	qPH4	RM241–G102				4.6	−0.8	6.9
	qPH5	R3166–RG360	3.9	−0.8	5.8			
	qPH6	C688–R1952b				5.3	0.7	5.1
	qPH10	RM228–C405a				9.8	−0.9	9.5
	qPH11	RG118–C794	5.2	−0.9	7.1			
				Multilocus	20.7			23.5
MRL	*qMRL3*	C316–C63				5.2	0.5	5.7
	qMRL5	R830–R3166	7.4	−0.4	8.6	6.1	−0.5	5.7
	qMRL7	RM234–R1789	7.4	−0.4	9.0			
	qMRL10	C1633–C677				6.6	−0.6	7.9
	qMRL11	C794–R2918	4.4	−0.3	4.5			
	qMRL11	RM254–G4001				3.9	−0.5	3.6
				Multilocus	19.6			19.8
SDW	*qSDW1*	C2340–C86				4.2	51.5	5.6
	qSDW2	RM240–RM213	4.4	−48.2	7.0			
	qSDW3	RG393–C1087				4.0	51.1	5.8
	qSDW5	R3166–RG360	10.2	−66.3	12.6	4.3	−52.5	6.2
	qSDW10	RG561–RM288				9.5	−76.1	13.1
	qSDW11	RG118–C794	4.0	−41.1	4.9			
				Multilocus	19.3			24.7
RDW	*qRDW2*	RM240–RM213	4.1	−3.9	6.4			
	qRDW3	RZ403–R19				7.3	23.3	6.7
	qRDW4	C820–C933				3.9	17.1	3.5
	qRDW5	R830–R3166	6.4	−6.0	8.7			
	qRDW5	R3166–RG360				12.0	−34.2	13.7
	qRDW10	RM228–C405a				7.5	−23.5	6.9
	qRDW11	RG118–C794	4.6	−5.4	7.1			
				Multilocus	20.3			22.4
TDW	*qTDW2*	RM240–RM213	4.6	−53.8	7.3			
	qTDW3	RZ403–R19				7.3	76.3	8.9
	qTDW5	R3166–RG360	10.3	−72.6	12.6	7.9	−87.0	10.8
	qTD10	RM228–C405a				9.4	−97.3	12.6
	qTDW11	RG118–C794	4.2	−45.7	5.0			
				Multilocus	21.4			
								23.6
RSR	*qRSR4*	C820–C933				8.3	1.6	11.1
	qRSR11	RM224–Y6854L	4.3	0.55	7.5			

[a] QTL nomenclature follows that of McCouch et al. 1997. PH, Plant height (cm); MRL, the maximum root length (cm); SDW, shoot dry matter weight (mg); RDW, root dry weight (mg); TDW, total dry weight (mg); RSR, root-shoot ratio

[b] Markers that are underlined were the nearest marker to the QTL

[c] Negative values indicate Minghui 63 alleles decrease trait values

was not related to any QTL of RDW and SDW, which are the component traits of RSR.

We were able to detect positive QTL alleles in the parent with the inferior phenotype. This was also achieved in our previous studies on mature rice plants (Yu et al. 1997; Xing et al. 2002) and in many other studies (de Vicente and Tanksley 1993; Asins et al. 1994; Redoña and Mackill 1996a, b, c). With the help of linked molecular markers, the pyramiding of positive alleles from both parents could be a more efficient way to improve rice plants.

Pleiotropic QTL and linked QTL

If two QTL peaks are situated very close to each other and the 1-LOD support intervals are completely or mostly overlapping, these two QTL would be regarded as being a single QTL having pleiotropic effects. However, we counted each QTL independently to simplify and clearly specify the number of QTL detected. Based on this assumption, three regions on chromosomes 2, 5, and 11 showed pleiotropic effects on seedling traits at 30 days. Pleiotropic effects of QTL in the vicinity of R3166 on the short arm of chromosome 5 were observed for PH, SDW, MRL, RDW, and TDW at 30 days post-sowing. QTL on chromosome 11 also showed pleiotropic effects on PH, MRL, SDW, RDW, and TDW during the first 30 days of seedling growth. Zhenshan 97 alleles at the two QTL expressed positive effects on the traits. Four regions on chromosomes 3, 4, 5 and 10 were observed to simultaneously affect different traits at 40 days post-sowing. The two regions on chromosomes 5 and 10 also had pleiotropic effects on MRL, SDW, RDW, and TDW in the first 40 days of seedling growth. These results are consistent with the high correlation coefficients between TDW, SDW, and RDW, indicating that a good root system (long MRL, high RDW, and a large number of roots) is associated with rapid shoot growth. At 40 days, a QTL with pleiotropic effects on RDW and TDW, located in the interval RZ403–R19, was closely linked to the QTL for SDW in the interval RG393–C1087.

For breeding purposes, the application of linked QTL and pleiotropic QTL should be carried out with care. For example, QTL with pleiotropic effects on SDW, RDW, and TDW on chromosomes 2, 3, 5, and 11 were also detected for grain yield, 1,000-grain weight, grains per panicle, and tillers per plant, respectively, in our previous study (Xing et al. 2002). The alleles from Zhenshan 97 at QTL on chromosomes 2, 5, and 11 increased all of the associated trait values, whereas the Zhenshan 97 alleles at the pleiotropic QTL on chromosome 3 increased 1000-grain weight but decreased grains per panicle. The regions in the vicinity of RZ403 on chromosome 3 and of R3166 on chromosome 5 largely affected grain shape (Tan et al. 2000). For these kinds of pleiotropic and linked QTL, the transfer of the ideal genotype of one QTL region could simultaneously improve a few traits, such as rapid shoot growth, rapid root growth, and total seedling biomass—if the pleiotropy and linkage are in the positive direction. For pleiotropy in the negative direction, however, it is very difficult to attain the ideal genotype. A careful determination of just which genotype could contribute most positively to rice production should be made. For linked QTL, in theory, the ideal genotypes could be obtained in a large population, although breaking the close genetic linkage is often expensive. Further research on the regions where QTL are concentrated, particularly those containing pleiotropic QTL—such as developing near-isogenic lines for gene fine mapping and cloning—should be very interesting in theory and useful for rice breeding programs.

Time-specific QTL

Sixteen and twenty QTL were detected for the six traits at 30 days and 40 days, respectively. Only four QTL for the four traits in the same region on chromosome 5 were detected in common. In fact, only one QTL with pleiotropic effects on four traits could be detected across the two stages. In other words, 12 QTL detected at 30 days were not identified at 40 days, and 16 new QTL were discovered at 40 days. Of the 16 QTL detected at 30 days, Minghui 63 alleles caused an increase in the corresponding traits at only two QTL, while at 40 days, Minghui 63 alleles showed an increase in trait values at eight of the 20 QTL.

These results are in agreement with the parents' developmental differences. Minghui 63 initiates panicle differentiation about 30 days later than Zhenshan 97, which initiates panicle differentiation about 33 days after being sown in the middle of June in Wuhan and flowers 25 days later (58 days from sowing to flowering). The period between 30 days and 40 days post-sowing is thus the transition stage of Zhenshan 97 from vegetative growth to reproductive growth. One explanation for the results is that the expression of some alleles for seedling growth from Zhenshan 97 are suppressed at the transition stage and the alleles controlling reproductive growth are activated but that some alleles from Minghui 63 for vegetative growth are still being expressed or are active at this stage. Thus, more alleles from Minghui 63 confer positive effects on trait expression at the late seedling stage. Our previous studies on mature rice plants found that more Minghui 63 alleles at QTL increased trait values (Yu et al. 1997; Xing et al. 2002).

Several investigators of time-related QTL mapping have reported the detection of different QTL at different growth stages, with only a few QTL detected at all stages (Price and Tomos 1997; Yan et al. 1998; Wu et al. 1999). Our present results are in agreement with these observations. For example, no common QTL for PH was detected at both stages. Moreover, there is no common QTL for plant height between the two seedling stages and the maturity stage (Xing et al. 2001). Only one QTL on chromosome 5 with pleiotropic effects on rice seedling traits was common to both stages. Price and Tomos (1997) found the two most significant QTL for maximum root growth on chromosomes 6 and 11, which appeared to display profoundly different developmental influences. The effect of the QTL on chromosome 6 was apparent at day 3, became larger on day 7, and then declined to nearly insignificant levels by day 28. The effect of the major QTL on chromosome 11, however, was not apparent until day 21 and became pronounced at day 28. Different time-related QTL (genes) significantly associated with some phenotypic traits could not be detected at all stages. This could be one of the main reasons why fewer QTL are identified for complex traits than would be expected at maturity.

QTL analysis based on near-isogenic lines can dissect the QTL into single Mendelian factor and distinguish pleiotropic QTL from linked QTL. Using the NILs from the same cross between Zhenshan 97 and Minghui 63, Xing et al. (2001) dissected one heading date QTL on chromosome 7 with moderate effect into a single Mendelian factor that has a greater effect than one from RILs. Using advanced backcross populations, the Japanese Rice Genome Program identified several heading date QTL, which have effects too small to be identified in F_2 populations (Lin et al. 1998, 2002; Yamamoto et al. 2000). Once mapped genes are isolated, the study of gene (QTL) expression can move from the genetic level into the phenotypic level.

Comparison with previously reported QTL for seedling traits

With the same RILs used in this study, Cui et al. (2002) detected QTL for seedling vigor traits, such as MRL, SDW, TDW, and RDW, in the first 10 days of seedling growth. A QTL in the vicinity of R3166 on chromosome 5 was also found to have pleiotropic effects on SDW, TDW, and RDW in the same direction. By comparing the genetic position of markers with a study done by Redoña and Mackill (1996c), we found that a region between RG173 and RM81A on chromosome that contained one QTL for PH also controlled mesocotyl length (Redoña and Mackill 1996c). QTL for SDW, RSW, and TDW were mapped to the flanking region of RZ403 on chromosome 3, and the same region harbored QTL for shoot length, coleoptile length, and mesocotyl length (Redoña and Mackill 1996c). A highly significant correlation was observed between SDW and RDW in the present study and in a previous study (Cui et al. 2002).

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