Indian J. Genet., 68(4): 366-372 (2008)

Dynamic mapping of QTLs for rice seedling growth

P. K. Pathak[1]

Department of Agronomy, Zhejiang University, Hua Jia Chi Campus, Hangzhou 310029, Peoples' Republic of China

(Received: February 2007; Revised: October 2008; Accepted: October 2008)

Abstract

QTLs associated with growth of rice seedling were mapped using a doubled-haploid (DH) population derived from a cross between lowland *indica* variety, IR64 and upland *japonica* variety, Azucena. Age-specific measures on seedling growth parameters such as seedling height, root depth, seedling weight, recorded at seven days interval, starting from 16th day of sowing, were used to detect the QTLs. A QTL mapping technique termed as 'conditional mapping' has been described and the utility of the technique has been illustrated. Altogether 11 QTLs each for seedling height and root depth and 10 QTLs for seedling weight were detected. The number of QTLs varied according to stages of growth indicating age-specific action of QTLs. The number of QTLs detected by conventional mapping at different stages of observation varied between 4 to 7 for seedling height and 2 to 4 for root depth and seedling weight with few QTLs for all the traits appearing consistently over the stages of observation. The conditional mapping technique allowed detection of three QTLs for seedling height and four QTLs each for root depth and seedling weight which remained undetected by the conventional mapping technique.

Key words: Rice (*Oryza sativa* L.), seedling height, root depth, seedling weight, quantitative trait loci (QTL), conditional mapping

Introduction

Rice is cultivated in a wide range of ecosystems under varying temperature and water regimes. Quick seedling growth and vigorous root system are important desirable traits for modern varieties of rice for all ecosystems, particularly, for upland situation. In rice, volumes of research findings have been reported in regards to QTL mapping for many important traits including seedling vigor [1-5] and root growth [6-13]. However, barring a few cases, QTL mapping efforts have been focused on a terminal character at a specific or final growth stage. This conventional mapping method allows identification of the QTLs based on the cumulative effects of the QTLs from initial time to the specific stage of observation without elucidating the effects of the QTLs during the period between two different growth stages. Such mapping method, therefore, can not fully reveal the QTLs controlling a trait, as the development of complex morphological structures is assumed to occur through actions and interactions of many genes that act differentially during ontogeny [14]. To gain better insight into the genetic control mechanism of complex quantitative traits, a dynamic QTL mapping method is needed, which can reveal the effect of QTLs within certain period of growth independent of the causal cumulative effects of the QTLs expressed preceding the specific period. Statistical methods have been proposed for analyzing conditional genetic effects and conditional genetic variance components [15]. Based on this statistical method, a mapping technique termed 'conditional mapping' has been proposed. This mapping technique permits detection of the QTLs based on the significant net effects of the QTLs expressed within a period of growth independent of the causal cumulative genetic effects prior to the reference period. The present study was undertaken to dynamically map the QTLs associated with seedling growth using both conventional and conditional mapping techniques.

Materials and methods

Plant material

A population of 105 doubled-haploid (DH) lines derived from a cross between a lowland *indica* variety, IR64 and an upland *japonica* variety, Azucena [16] was used in this study. A molecular map of this population was previously developed from an initial population of 135 DH lines with 175 polymorphic markers covering 2005 cM [17, 18].

[1]Present address: Department of Plant Breeding and Genetics, Assam Agricultural University, Jorhat 785013

Hydroponic evaluation for seedling growth

Twenty pre-germinated seeds of all the DH lines and the parents were sown in 10 cm-diameter plastic pots half filled with coarse sand and allowed to grow for 9 days under favorable temperature condition (25°-30°C). Nine days old (d) seedlings were carefully uprooted, roots were washed without damage and then the seedlings were transferred to hydroponic system [19] and allowed to grow. The seedlings wrapped at the base above the rooting regions with pieces of spongy material were fitted through the holes on plastic trays with a single seedling per hole. The plastic trays were placed on plastic boxes (65 cm long, 43 cm wide and 12.5 cm deep) allowing the roots to dip into the nutrient solution. Every plastic tray had 10 x 7 equally spaced holes of 25 mm diameter accommodating 10 DH lines, with 7 seedlings each. The nutrient solution was prepared together for all the boxes. Every morning, the tray position in relation to the boxes was changed, nutrient solution was added to maintain a constant level and the pH of the solution was adjusted at 5 to 5.5. At 7 days intervals, the nutrient solution was replaced to maintain the nutrient status at the required level. Starting from 16d (7 days after transferring the seedlings to hydroponic system), every 7 days interval, observations were recorded on the seedlings for seedling height, root depth and seedling weight.

QTL analysis

QTLs for seedling growth at different stages of observation were detected and mapped on the chromosomes using QTLMAPPER V.1 [20], developed on mixed-model based composite interval mapping (MCIM) [21]. The QTLs, thus identified, were detected based on the cumulative effect of the QTLs from the initial time to the specific stage at which the observation was made. Such QTL mapping, however, does not fully reflect the dynamic mode of gene action in agreement with the model of genetic control of developmental traits. To detect the QTLs based on their effects between two stages of growth, independent of the gene effects prior to the specified period, conditional mapping was adopted where, QTL analysis was performed with the phenotypic mean at time t conditional on the phenotypic mean at time (t – 1) [$y_{(t|t-1)}$]. The conditional phenotypic value $y_{(t|t-1)}$ of an individual genotype in the DH population can be partitioned as:

$$y_{k(t|t-1)} = \mu_{(t/t-1)} + a_{i(t|t-1)}\, x_{A_{ik}} + a_{j(t|t-1)} x_{A_{jk}} + aa_{ij(t|t-1)} x_{AA_{ijk}} + \sum_f u_{M_{fk}}\, e_{M_{f(t|t-1)}} + \sum_f u_{MMlk}\, e_{MM_{l(t|t-1)}} + \varepsilon_{k(t|t-1)} \quad (1)$$

where, $y_{(t|t-1)}$ is the phenotypic value of the k-th individual (k = 1, 2,..., n) at time t conditional on the phenotypic value at time (t–1); $\mu_{(t|t-1)}$ is the conditional population mean; $a_{i(t|t-1)}$ and $a_{i(t|t-1)}$ are the conditional additive effects (final effect) of two putative QTLs, respectively $aa_{ij(t|t-1)}$ is the conditional additive x additive epistatic effect (fixed effect) between two QTLs; $x_{A_{ik}}$, $x_{A_{jk}}$ and $x_{AA_{ijk}}$ are coefficients of QTL effects derived according to the observed genotypes of the markers and the testing points; $e_{M_{f(t|t-1)}} \sim N(0, \sigma_M^2)$ is the conditional effect of marker f with coefficient $u_{M_{fk}}$; $e_{MM_{l(t|t-1)}} \sim N(0, \sigma^2_{MM})$ is the conditional effect of the l-th marker interaction with coefficient $u_{MM_{lk}}$ and $\varepsilon_{k(t|t-1)} \sim N(0, \sigma^2_e)$ is the conditional residual effect at time t. The conditional phenotypic value [$y_{(t|t-1)}$] was obtained by using the statistical method proposed for genetic analysis of developmental traits [15]. The QTLs detected by this conditional mapping would reflect the action of genes during the time period from (t–1) to t. The LR threshold for declaring significance for QTL additive effects was fixed at P = 0.005.

Results and discussion

The mean phenotypic values of the parents and the DH population for the traits at different days of observation are presented in Tables 1 and 2, respectively. The parents differed significantly for the traits from 23d onwards and the population distributed normally for all the traits at all the stages of observation with skew and kurt values being less than 1 (Table 2) suggesting that

Table 1. Phenotypic mean values of the parents for different seedling traits at five stages of growth

Traits	Stages	IR64	Azucena
Seedling height (cm)	16d	24.63±1.23	23.27±1.46
	23d	39.86±2.06	44.09±2.12
	30d	51.01±1.59	64.51±2.83
	37d	53.11±1.11	72.61±3.43
	44d	58.81±2.96	82.03±5.57
Root depth (cm)	16d	12.96±3.14	12.50±0.64
	23d	13.30±1.60	21.54±2.78
	30d	16.89±1.68	22.94±1.85
	37d	18.21±2.06	24.31±1.94
	44d	18.54±2.00	24.50±2.12
Seedling weight (g)	16d	0.32±0.02	0.36±0.04
	23d	2.01±0.06	1.89±0.08
	30d	4.98±0.42	4.38±0.37
	37d	7.40±0.64	7.04±0.58
	44d	11.42±0.83	11.89±1.00

Table 2. Phenotypic values of the DH population for different seedling traits at five stages of growth

Traits	Growth stages	Mean	Range	Skew	Kurt
Seedling height (cm)	16d	24.00±3.75	16.15-34.65	0.27	–0.26
	23d	36.54±5.05	27.07-52.50	0.32	0.12
	30d	51.13±7.33	34.67-72.19	0.27	–0.05
	37d	58.46±9.35	36.91-84.20	0.23	–0.15
	44d	65.45±11.37	43.04-96.62	0.16	–0.40
Root depth (cm)	16d	12.00±2.19	7.58-18.32	0.73	0.33
	23d	14.76±2.15	10.33-21.66	0.44	0.50
	30d	18.35±2.57	11.61-27.44	0.13	0.56
	37d	19.69±2.91	12.46-28.36	0.14	–0.04
	44d	20.88±2.74	14.23-28.40	0.28	–0.10
Seedling weight (g)	16d	0.32±0.06	0.19-0.49	0.42	0.14
	23d	1.70±0.39	0.94-2.75	0.47	–0.36
	30d	4.04±1.04	2.25-6.71	0.49	–0.38
	37d	6.73±1.96	3.11-11.82	0.53	–0.27
	44d	11.35±4.10	3.99-22.67	0.50	–0.26

the data were suitable for QTL analysis. Transgressive segragants were observed in the population for all the traits in all the stages of observation (Tables 1 and 2).

In the study, 11 QTLs each for seedling height and root depth and 10 QTLs for seedling weight were detected through conventional and conditional mapping approaches (Tables 3, 4, 5 and Fig. 1). However, most of the QTLs, *viz.,* eight, seven and six QTLs for seedling height, root depth and seedling weight, respectively were detected by conventional mapping only. Moreover, the QTLs, thus detected, varied according to the stages of growth, the number ranging between 4 to 7 for seedling height and 2 to 4 for both root depth and seedling weight with few QTLs appearing consistently over the stages of observation. This provides clear evidence of age-specific action of the QTLs in full agreement with the results reported from both classical genetic analyses [22-24] and QTL mapping studies [25-27]. Again, for the QTLs detected consistently over the stages of growth, the magnitude of effects and contribution to the phenotypic variation differed according to the stages implying that the relative importance of the QTLs appearing over the trait's developmental path might vary according to the stages. Such results justify the need to adopt a dynamic approach to mapping QTLs for developmental traits to detect, on one hand, the QTLs expressed at different stages of growth without chance of any QTL being missed owing to their age-specific expression and, on the other, to understand the relative importance of few QTLs playing the key role in shaping the phenotype. For instance, it has been seen that among all the QTLs detected for seedling height, four QTLs (Sh1-2, Sh2-2, Sh3-1 and Sh8-1), identified by conventional mapping throughout the seedling-growing period, are of considerable importance. Interestingly, three QTLs located in the positions of these QTLs except Sh8-1 were found in the same DH population to be consistently associated with plant height at almost all the stages of growth after transplanting [26] with the corresponding QTLs affecting the traits in the same direction. This might represent a very tight linkage between two sets of genes or positive pleiotropic effects of the same gene on the two traits. Such tight linkage or pleiotropic relation of several important genes may be the basis of the strong positive correlation between seedling height and plant height. Of course, difference in appearance of several QTLs in the same DH population for height at the seedling stage of growth in the present study and at the latter stages of growth after transplanting in earlier studies [26, 28] indicates to the possibility of breeding rice varieties of desired seedling and plant height. Thus, a dynamic mapping approach would help elucidating the genetic basis of the relationship among traits in growth and development, which, in turn, could guide the breeders to formulate appropriate breeding strategies.

In the QTLs detected, alleles from either of the parents affected seedling growth positively depending on the QTLs. However, each of the QTLs, when detected at more than one stage, affected the trait in the same direction during the entire seedling growth period. The relative contributions of the individual QTLs [$H^2(a_j)$] detected by conventional mapping to the total phenotypic variation ranged from as low as 3 per cent to as high as 29 per cent for seedling height, 3 to 30 per cent for root depth and 3 to 22 per cent for seedling

Table 3. Estimated additive genetic effects (and contributions to the phenotypic variation) of the QTLs detected for growth of seedling height (cm)

Chr.	QTL	Marker interval	Dist.(cM)	Conventional mapping					Conditional mapping			
				16d	23d	30d	37d	44d	23d/16d	30d/23d	37d/30d	44d/37d
1	Sh1-1	RG146-RG345	34.0		–1.46** (10)	–1.75** (05)		–2.47** (03)				
1	Sh1-2	RZ730-RZ801	30.0	–2.01** (29)	–1.39* (09)	–3.81** (22)	–5.48** (23)	–7.83** (29)				
2	Sh2-1	RG171-RG157	2.0							–0.94** (10)		
2	Sh2-2	Amy1A/C-RG95	6.0	1.58** (18)	1.29** (08)	2.47** (09)	3.96** (12)	6.34** (19)				
3	Sh3-1	CDO 87-RG910	4.0	–1.33** (10)	–1.41** (09)	–2.29** (08)	–4.57** (16)	–4.11** (08)				
6	Sh6-1	Amy2A-RG433	4.0			1.59** (04)		2.46** (03)				
7	Sh7-1	RG773-RG769	24.0								1.05** (17)	
8	Sh8-1	Amp_2-CDO99	4.0	1.17* (10)	1.82** (15)	1.82** (05)	3.76** (11)	4.67** (10)				
9	Sh9-1	CDO590-C711	2.0					–2.32** (03)				
9	Sh9-2	RG667-RG451	10.0						1.08* (15)			0.97** (11)
12	Sh12-1	RG958-RG181	0.0			–2.66** (11)						
$H^2(\Sigma a_i)$				66	49	64	63	76	15	10	17	11

* and ** represent significance levels of P = 0.005 and 0.001, respectively; '+' and '–' indicate that IR64 and Azucena alleles respectively, affect the trait positively, the distance indicates the putative position of the QTLs at an estimated distance measured in cM from the left one of the markers bracketing the concerned QTL and first digit in the notation for QTL indicates chromosome no. bearing the QTL

Table 4. Estimated additive genetic effects (and contributions to the phenotypic variation) of the QTLs detected for growth of root depth (cm)

Chr.	QTL	Marker interval	Dist.(cM)	Conventional mapping					Conditional mapping			
				16d	23d	30d	37d	44d	23d/16d	30d/23d	37d/30d	44d/37d
1	Rd1-1	RG345-RG381	2.0					0.73** (06)				
2	Rd2-1	RG171-RG157	0.0								0.37** (11)	
2	Rd2-2	RZ318-Pall	4.0	–0.89** (16)	–0.98** (19)	–1.32** (19)	–1.65** (30)	–1.63** (30)	–0.68** (08)	–0.66** (17)		
2	Rd2-3	RG95-RG654	4.0		0.69** (09)							
6	Rd6-1	RG162-RG172	4.0			0.53* (03)						
7	Rd7-1	PGMS0.7-CDO59	0.0							0.43** (07)		
8	Rd8-1	RG978-RG1	6.0	–0.83** (14)	–0.82** (13)							
8	Rd8-2	RG1-Amy3D/E	2.0									0.59** (22)
9	Rd9-1	RG667-RG451	18.0							0.48** (09)		
10	Rd10-1	G1084-RG257	0.0		0.65** (08)		0.97** (10)		0.99** (18)			
11	Rd11-1	RG103-RG1109	10.0			–1.15** (14)				–0.77** (23)		
$H^2(\Sigma a_i)$				30	46	35	39	36	27	56	11	22

* and ** represent significance levels of P = 0.005 and 0.001, respectively; '+' and '–' indicate that IR64 and Azucena alleles respectively, affect the trait positively, the distance indicates the putative position of the QTLs at an estimated distance measured in cM from the left one of the markers bracketing the concerned QTL and first digit in the notation for QTL indicates chromosome no. bearing the QTL

weight. The cumulative contributions of the QTLs [$H^2(\Sigma a_j)$] detected at different stages varied from 49 to 76 per cent for seedling height, 30 to 46 per cent for root depth and 32 to 53 per cent for seedling weight.

Conditional mapping, in the present study, helped to identify three QTLs for seedling height and four QTLs each for root depth and seedling weight which were not detected by conventional mapping technique (Tables 3, 4, 5 and Fig. 1). Similar results were reported for plant height and tiller number also [26, 27]. Such results suggest that the genes act differentially during ontogeny. Since the detection of QTLs by conventional mapping is based on the accumulated effects of the QTLs over a long period, the variation in the population caused by such cumulative effects can be made insignificant by the mutually opposite effects of the same QTL or closely located QTLs expressed at different time thus rendering the QTL undetectable by conventional mapping. The hints that the same QTL may act differentially at different stages of growth have come from the present study itself. Two QTLs associated with root-depth, one identified by conventional (Rd8-1) and the other identified by conditional mapping (Rd8-2), were located very close to each other and affected the trait in different directions. These two QTLs might represent two tightly linked loci or might be the case of negative pleiotropism of one individual locus at different stages of growth. It was earlier also reported that the individual QTL might have opposite genetic effects on the same trait at different stages of growth [26, 27]. Quantitative genetic studies in mice also indicated that individual genes might have opposite pleiotropic effects on the early and late growth [29].

The study has demonstrated very well that the dynamic approach to conventional mapping in conjunction with conditional mapping would allow to clearly reveal the gene system associated with the developmental traits for formulation of appropriate breeding strategies to bring about desired genetic improvement.

Acknowledgments

The author sincerely thanks Prof. Zhu Jun, Zhejiang University, Hangzhou, PR China for his kind help and guidance.

Table 5. Estimated additive genetic effects (and contributions to the phenotypic variation) of the QTLs detected for growth of seedling weight (g)

Chr.	QTL	Marker interval	Dist.(cM)	Conventional mapping					Conditional mapping			
				16d	23d	30d	37d	44d	23d/16d	30d/23d	37d/30d	44d/37d
1	Sw1-1	RG810-RG331	6.0	–0.024** (14)	–0.184** (22)	–0.408** (14)	–0.642** (13)					
2	Sw2-1	RG437-RG544	12.0	0.016** (06)								
2	Sw2-2	Pall-RZ58	10.0								0.194** (11)	
3	Sw3-1	CDO 87-RG910	0.0	–0.011* (03)	–0.115** (08)	–0.416** (14)		–1.581* (18)				
4	Sw4-1	RG190-RG908	8.0				0.565** (10)	1.349** (13)				
4	Sw4-2	RG449-RG788	10.0								0.428** (11)	
5	Sw5-1	RZ67-RZ70	0.0	0.024** (14)	0.149** (14)	0.379** (12)	0.748** (17)					
8	Sw8-1	Amy3DE-RZ66	20.0						0.088** (17)			
8	Sw8-2	Amp_2-CDO99	10.0		0.100** (06)	0.387** (06)						
10	Sw10-1	RZ625-CDO93	2.0						–0.045* (04)			
$H^2(\Sigma a_j)$				38	51	53	40	32	22	0	22	0

* and ** represent significance levels of P = 0.005 and 0.001, respectively; '+' and '–' indicate that IR64 and Azucena alleles respectively, affect the trait positively, the distance indicates the putative position of the QTLs at an estimated distance measured in cM from the left one of the markers bracketing the concerned QTL and first digit in the notation for QTL indicates chromosome no. bearing the QTL

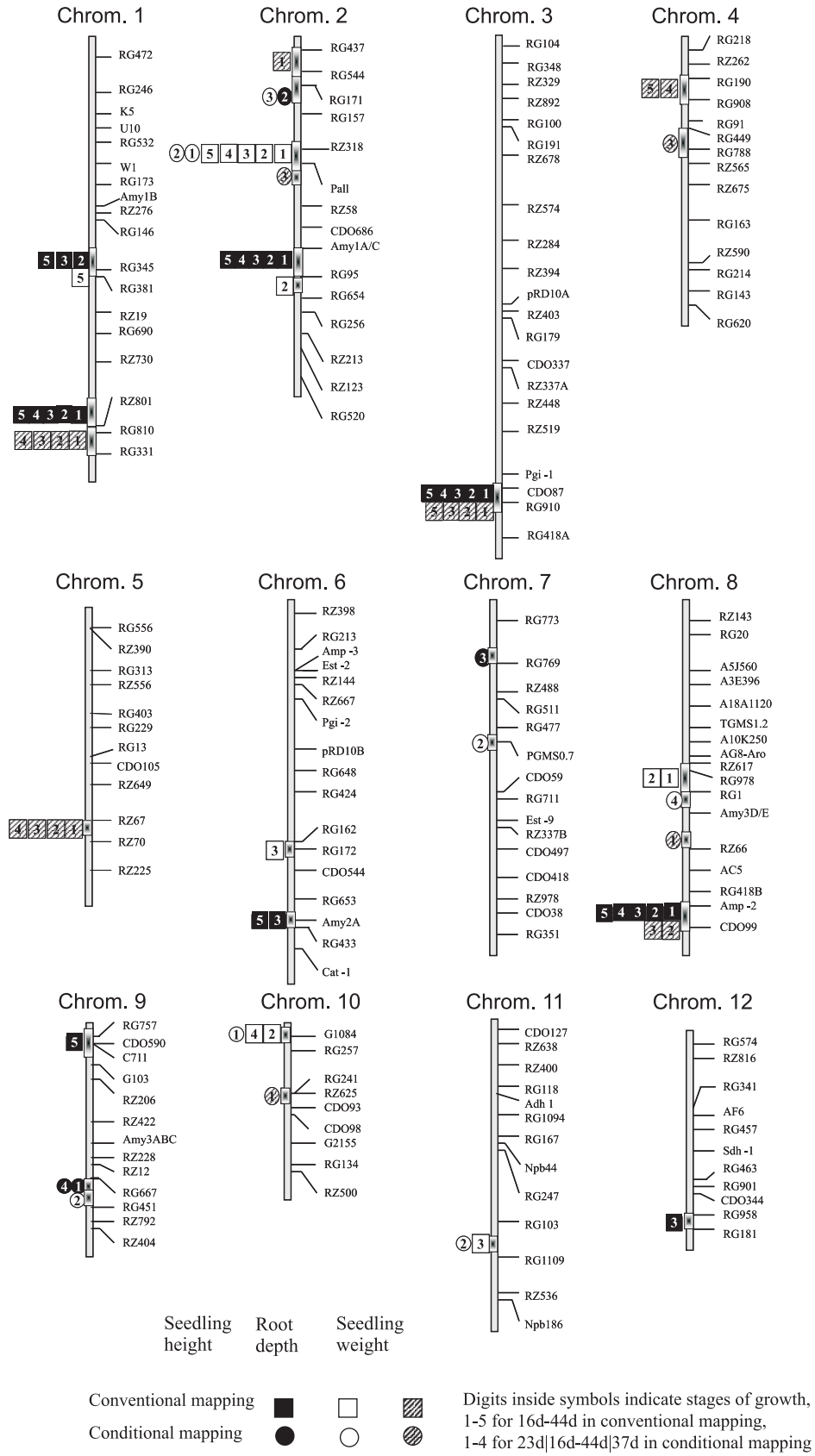

Fig. 1. Linkage map showing putative QTLs associated with seedling growth

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