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Dynamic analysis of QTL for plant height at different developmental stages in maize (*Zea mays* L.)

YAN Jianbing[1], TANG Hua[1], HUANG Yiqin[1], SHI Yonggang[2], LI Jiansheng[3]& ZHENG Yonglian[1]

1. National Key Lab of Crop Genetic Improvement, Huanzhong Agricultural University, Wuhan 430070, China;
2. Xiangfan Chia-Tai Agricultural Development Co., LTD., Xiangfan 441104, China;
3. National Maize Improvement Center of China, China Agricultural University, Beijing 100094, China

Correspondence should be addressed to Zheng Yonglian (e-mail: yonglian.zheng@263.net)

Abstract **Plant height in maize is not only one of important agronomic traits, but also one of model traits suitable for study of developmental biology. Using data from field tests in two locations (Wuhan and Xiangfan) within the same year and a molecular linkage map covering all of 10 chromosomes, QTLs affecting plant height at five different developmental stages were mapped and analyzed by the combination of composite interval mapping and the conditional analysis method. Eight QTLs for plant height at different stages were located at different regions of five chromosomes (LOD≥2.5). The results showed that there were different effect values of QTL on plant height at different developmental stages. Three QTLs were detected at all of five stages. With different stages, contributory percentage of single QTL to plant height varied between 3.8% and 17.1%. It suggested that the expression of each QTL controlling plant height was different at different stages. With net growth, seven conditional QTLs for plant height were detected. Conditional QTLs were nearly detected at each stage, and QTLs of Ph1-1, Ph1-2, Ph3, Ph5-2 and Ph9 were detected at both locations (Wuhan and Xiangfan). The contributory percentage of single conditional QTL to plant height varied between 3.8% and 12.3%, indicating that QTLs for plant height are expressed in different time-space. Therefore, QTL expressed at different stages should be considered when marker assistant selection is conducted for quantitative traits.**

Keywords: maize, plant height, QTL, developmental quantitative genetics.

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Plant height is one of important agronomic traits in maize breeding. In the past few years, to increase the planting density and prevent plants from lodging, studies on the genetic mechanism of plant height were given great attention to. Since the 1990s, molecular markers have provided a powerful tool to study the trait of plant height at the molecular level[1—3]. But most of research for plant height only focused on data at mature stage. Till now, about 70 genes or QTLs have been located[4]. Moreover, some genes have been even cloned[5—7]. During the vegetative growth period, plant height grows about 2.5 cm per day from elongation stage to a little tubaeformis stage, about 10 cm per day from a little tubaeformis stage to tasseling stage, and about 1 cm per day after silking. After pollination, however, the plant height remains constant[8]. Recently, the combination of developmental quantitative genetics and molecular linkage map makes it possible to analyze the developmental behavior of important agronomic traits[9—13]. However, there is yet no report about the dynamic analysis of QTL for plant height in maize. In this investigation, we attempt to analyze QTL for plant height at different developmental stages and provide some useful information for further understanding the genetic mechanism of plant height in maize.

1 Materials and methods

(ⅰ) Materials. 266 $F_{2:3}$ families derived from F_2 individuals of Zong 3×87-1, which is widely extended to elite hybrid, were used as a mapping population. Young leaves of F_2 individuals were collected to store at −70℃ for extraction of DNA samples.

(ⅱ) Field experiments. In the spring of 2000, $F_{2:3}$ families was planted in green house, and then transplanted into the field at three-leaf stage. Field tests were performed on the farm of Huazhong Agricultural University, Wuhan, and in the experimental station of Chia-Tai Agricultural Developmental Co. LTD., Xiangfan, respectively. According to the randomized complete block design, each field plot included 20 plants growing in a single row of 5 m in length with 0.70 m in width between each two rows. In the tubaeformis stage, the height of 10 plants counted continuously from the third plant in each block was measured during every three days in Wuhan from June 7th to 19th, and in Xianfan from June 10th to 22nd, respectively. The average value was designated as observation of plant height. Before tassel grew out of the tubaeformis, the height referred to the distance from ground to tubaeformis; after tassel grew out of the tubaeformis, the height was defined as the distance from the ground to the top of tassel.

(ⅲ) Construction of linkage map. The total DNA samples of parents and F_2 individuals were extracted as the procedure described by Saghai et al.[14]. 459 markers including SSR and RFLP were selected for screening polymorphism between two parents. SSR analysis followed the method described by Senior et al.[15] and RFLP analysis was conducted according to Gardiner et al.[16]. A molecular linkage map was constructed by using Mapmaker 3.0[17].

(ⅳ) Data analysis. The unconditional QTLs for plant height were located with the composite interval

mapping method[18]. The QTL detected by unconditional mapping reflected the total effect of gene expression from seeding to the time *t*. QTL for growth behavior of plant height was determined by the combination of the composite interval mapping method and conditional analysis method[19]. The QTL detected by this method reflected the net effect of gene expression from time *t*–1 to time *t*. The unconditional QTL detected at the first testing stage was also the conditional QTL from the seeding to the first testing stage. The QTL located according to the data measured at different stages was called as unconditional QTL. QTL located on the basis of the net growth at different stages was called as conditional QTL[12,13]. The software of QTL Cartographer Version 1.30 was used to locate QTL (LOD≥2.5) [20].

2 Results

(ⅰ) Analysis of plant height. The plant heights of parents and $F_{2:3}$ population in two experimental locations are shown in Tables 1 and 2. In the former 4 stages, the heights of parental plant grew very fast (Tables 1 and 2). In the earlier stage, Zong3 grew faster than 87-1, but slower in later stage. However, at the final stage, there was no significant difference on plant height between two parents. The plant heights of $F_{2:3}$ population varied greatly and fitted a normal distribution. For example, in the last stage, the minimum of plant heights of the population in Wuhan was 131.1 cm and the maximum 243.8 cm, with the average of 186.1 cm; In Xiangfan, the minimum plant height of the population was 130.7 cm and the maximum 221.1 cm, with the average of 185.7 cm, indicating that the plant growth of parents show a dynamic developmental difference.

(ⅱ) Construction of molecular marker linkage map. 150 SSR and 24 RFLP markers showing co-dominant segregation were employed for constructing a linkage map. The polymorphic markers were assigned into 12 linkage groups by Mapmaker 3.0, which cover 10 chromosomes of maize. The linkage map had a total length of 2531.6 cM and an average interval of 14.5 cM (Fig. 1), which was consistent with other maize linkage maps in marker alignments and intervals. 25 markers distributed on 10 chromosomes displayed a deviation of 1∶2∶1 by χ^2 test.

(ⅲ) Dynamic analysis of QTL for plant height. Using data from different stages, eight unconditional QTLs (LOD≥2.5) were detected by the composite interval mapping. These QTLs were named as Ph1-1, Ph1-2, Ph3, Ph5-1, Ph5-2, Ph5-3, Ph8 and Ph9 and located on 1st, 3rd, 5th, 8th and 9th chromosomes respectively. All of them were detected according to data from Wuhan and Xiangfan respectively, but had different effect values at different stages. The contributory percentage of single QTL varied between 3.8% and 17.1% (Fig. 1, Tables 3 and 4). Three QTLs (Ph1-1, Ph3 and Ph8) could be detected at all testing stages in Wuhan. However, Ph1-1 and Ph8 could be detected only at the 4th or 2nd testing stages in Xiangfan (Fig. 1). The additive value of Ph1-1 was above 10 at all stages in Wuhan and at the 4th of 5th testing stages in Xiangfan (Tables 3 and 4). The alleles from a parent of 87-1 had the positive effect on increasing plant height. The contributory percentage of ph1-1 was 8.2% at the last stage in Wuhan and 17.1% in Xiangfan. Similarly, the additive value of Ph3 was over six at all testing stages. It showed an increasing effect derived from the alleles of another patent, Zong3, on plant height. Unconditional QTL analysis indicated that the numbers of QTL affecting plant height at different stages were more than those at the last stage. In another word, some QTLs could be detected in certain stages but not at the last stage. For example, Ph1-2 could be detected in the three earlier testing stages in both Wuhan and Xiangfan; however, it could not be detected in the last stage. Another example is that the additive value of Ph9 was –2.1, 0.3, and 1.3 on June 10, June

Table 1 Plant height of $F_{2:3}$ population and two parents at different stages (Wuhan) (unit: cm)

Wuhan Date	Parents		$F_{2:3}$ population			
	Zong3 ± SD	87-1±SD	Min.	Max.	F_1±SD	Mean ± SD
06-04	110.2±14.7	106.5±12.8	86.5	177.3	167.9±24.4	136.8±17.6
06-07	130.6±12.0	123.8±13.1	105.4	207.3	209.0±23.8	160.6±17.2
06-10	147.6±10.8	149.7±11.5	115.1	221.8	231.3±12.5	174.2±17.9
06-13	155.3±11.2	158.5±12.1	130.5	234.1	233.8±10.6	182.6±17.8
06-16	156.3±11.3	160.8±11.8	131.1	243.8	233.8±10.6	186.1±18.2

Table 2 Plant height of $F_{2:3}$ population and two parents at different stages (Xiangfan) (unit: cm)

Xiangfan Date	Parents		$F_{2:3}$ population			
	Zong3±SD	87-1±SD	Min.	Max.	F_1 ± SD	Mean±SD
06-10	105.5±12.7	94.3±10.3	68.0	169.5	172.5±18.8	126.8±24.8
06-13	117.4±13.1	103.3±11.6	71.5	188.5	195.4±17.2	144.2±21.1
06-16	132.4±11.8	116.9±14.2	91.0	205.5	219.7±11.5	161.4±22.3
06-19	146.3±12.6	151.1±15.4	105.8	212.3	228.1±7.3	177.4±21.6
06-22	151.6 ± 11.0	163.2 ± 8.3	130.7	221.1	230.8 ± 8.0	185.7±19.9

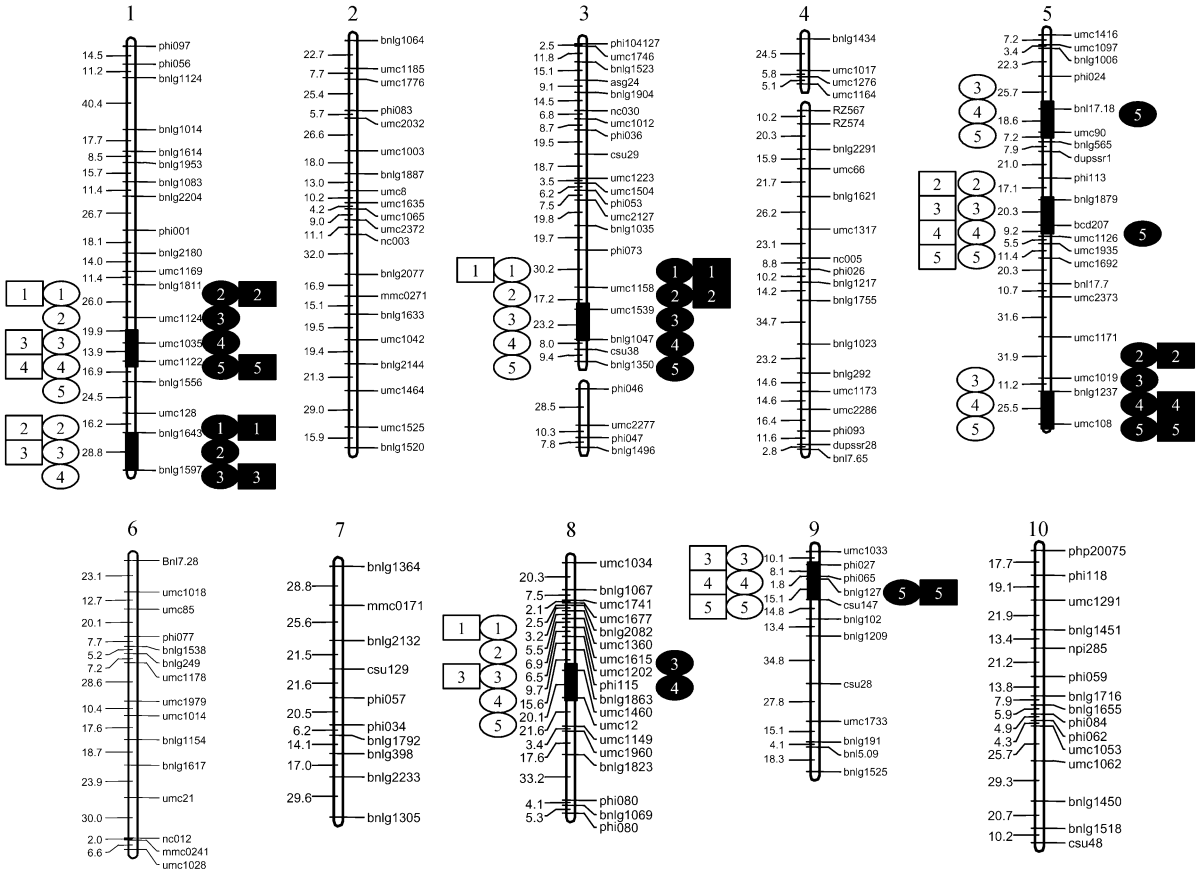

Fig. 1. QTL affecting plant height at different testing stages in maize. ▮ Location of QTL on chromosome; ① unconditional QTL detected at different stages in Wuhan; ❶ unconditional QTL detected at different stages in Wuhan; [1] QTL detected at different stages in Wuhan; ▮1 QTL detected at different stages in Xiangfan.

13, and June 16 respectively. That suggested that the alleles from parent 87-1 had the positive effect on plant height on June 10; and the alleles from parent Zong3 had the positive effect on plant height on June 13 and June 16. It implied that there was new expression of Ph9 or new gene affecting plant height from June 10 to June 13. The difference of unconditional QTL numbers and effect demonstrated that the expression of QTL affecting plant height was different at different stages. Based on the unconditional QTL analysis, the accumulative effect of QTL could be evaluated from seeding time to *t* time but the net expression or genetic effect of QTL could not be evaluated from time *t* to time *t*–1.

QTL analysis of *t* time by giving the phenotypic value of *t*–1 time is helpful to estimate QTL net expression effect at the given time and to locate QTL on chromosome, and is considerably beneficial for the molecular biology study of the time-space expression for QTL controlling plant height. By the combination of conditional analysis and composite interval mapping method, seven conditional QTLs affecting the plant height were detected, and five of them (Ph1-1, Ph1-2, Ph3, Ph5-2 and Ph9) could be detected in both Wuhan and Xiangfan. The contributory percentage of single QTL varied between 3.8% and 12.3%. The conditional QTL could be detected at nearly all-testing stages (Tables 3 and 4), indicating that the genes affecting the plant height expressed differently at different developmental stages and that plant growth was a gradual process. At the same time, there was a noticeable phenomenon that more conditional QTLs could be detected in a special time (June 7—10 in Wuhan; June 10—13 in Xiangfan). It suggested that genes expressed more actively in that time. The plant grew fastest during those stages when the plant developed from big tubaeformis stage to silking stage.

3 Discussions

According to the final data in this study, there are some differences of plant heights in the $F_{2:3}$ population between Wuhan and Xiangfan. These differences seemed to derive from G×E. However, the analysis by QTL Mapper2.0 revealed that only one QTL showed obvious interaction with environment at $P<0.01$ level (unpublished data) although six of seven unconditional QTLs

Table 3 Effects of QTL for plant height at different stages in Wuhan

QTL[a)]	Flanking markers	b)	6-4				6-7				6-10				6-13				6-16			
			A[c)]	D[d)]	LOD[e)]	R2[f)]	A	D	LOD	R2	A	D	LOD	R2	A	D	LOD	R2	A	D	LOD	R2
Ph1-1	umc1035-umc1122	*t*	−10.2	2.9	3.6	7.3	−11.5	3.3	3.9	9.3	−12.1	5.9	3.7	10.0	−11.3	3.7	5.3	9.2	−11.2	3.6	5.2	8.2
		t/*t*−1	−10.2	2.9	3.6	7.0					0.7	3.3	3.5	6.3	−1.3	−0.7	3.1	5.0				
Ph1-2	bnlg1643-bnlg1597	*t*					−8.5	8.9	2.8	10.4	−8.9	12.6	3.5	15.6	−6.6	12.6	3.0	13.6				
		t/*t*−1					−10.2	2.9	3.6	7.3	−3.5	−1.1	2.6	5.1								
Ph3	umc1539-bnlg1047	*t*	7.8	−1.3	2.7	5.0	9.2	−0.5	6.3	11.6	8.6	0.1	5.5	10.1	7.4	0.4	5.3	8.3	6.6	2.9	5.4	9.1
		t/*t*−1	7.8	−1.3	2.7	5.0																
Ph5-1	bnl17.18-umc90	*t*									−6.8	3.4	3.4	5.3	−6.9	0.9	4.7	6.8	−7.2	0.5	5.5	7.5
		t/*t*−1																				
Ph5-2	bnlg1879-bcd207	*t*					−7.0	2.0	3.5	5.0	−7.1	0.7	4.0	5.7	−9.2	1.6	6.4	8.9	−8.4	0.8	5.3	8.6
		t/*t*−1					−7.0	2.0	3.5	5.0	−4.0	0.4	5.4	10.2	−2.4	1.2	2.7	5.1	−4.1	2.2	8.6	14.3
Ph5-3	bnlg1237-umc108	*t*									−7.3	3.4	2.7	5.4	−8.0	3.0	3.7	6.6	−7.6	2.4	3.7	6.0
		t/*t*−1																				
Ph8	bnlg1863-umc1460	*t*	2.9	3.1	2.6	3.8	3.2	2.7	2.8	3.9	4.0	2.5	3.0	4.5	4.5	2.0	3.3	4.6	5.1	1.7	3.4	4.8
		t/*t*−1	2.9	3.1	2.6	3.8					2.7	−1.8	2.9	6.2								
Ph9	phi027-phi065	*t*									−2.1	7.7	3.1	4.8	0.3	8.0	4.8	7.2	1.3	8.0	5.2	7.8
		t/*t*−1									−1.5	3.9	3.2	5.7	2.1	0.1	2.7	4.4	1.4	0.4	3.0	5.3

a) Numbers following the two letters represent the chromosome locations of the QTL; b) *t* is the cumulative effects at time *t*, *t*/*t*−1 is the effect from time *t*−1 to *t*; c) additive effect; positive values of the additive effect indicate that the Zong3 alleles are in the direction of increasing the plant height; d) dominance effect; positive values of the dominance effect indicate that the heterozygotes have higher phenotypic values than the respective means of two homozygotes; e) log-likelihood value calculated by composite interval mapping; f) phenotypic variation explained by each QTL.

Table 4 Effects of QTL for plant height at different stages in Xiangfan

QTL[a)]	Flanking markers	b)	6-10				6-13				6-16				6-19				6-22			
			A[c)]	D[d)]	LOD[e)]	R2[f)]	A	D	LOD	R2	A	D	LOD	R2	A	D	LOD	R2	A	D	LOD	R2
Ph1-1	umc1035-umc1122	*t*					–12.2	4.3	3.9	7.1	–15.7	5.8	6.0	10.7	–17.3	5.2	8.0	13.3	–15.1	0.8	11.4	17.1
		t/*t*–1					–12.2	4.3	3.9	7.1									–2.2	–0.2	3.2	4.9
Ph1-2	bnlg1643-bnlg1597	*t*	–6.3	2.4	3.8	6.3	–9.8	9.7	2.9	8.9	–10.6	10.4	3.3	10.3								
		t/*t*–1	–6.3	2.4	3.8	6.3					–14.5	5.6	5.1	9.2								
Ph3	umc1539-bnlg1047	*t*	6.5	4.0	4.6	12.3	7.5	0.5	4.2	8.5	6.7	2.1	4.0	8.6	7.0	0.2	3.9	7.3	5.2	3.1	5.3	9.2
		t/*t*–1	6.5	4.0	4.6	12.3	6.8	–0.5	2.8	5.9												
Ph5-1	bnl17.18-umc90	*t*																	–6.4	1.4	3.4	4.8
		t/*t*–1																				
Ph5-2	bnlg1879-bcd207	*t*																	–6.2	0.7	3.3	4.9
		t/*t*–1																				
Ph5-3	bnlg1237-umc108	*t*					–13.8	3.2	3.2	15.5	–9.5	7.4	3.2	8.8	–8.9	4.5	2.6	6.3	–11.8	4.8	4.5	12.4
		t/*t*–1					–8.3	5.8	3.4	6.0					–3.6	1.0	4.2	7.5	–1.7	–2.2	4.5	7.2
Ph8	bnlg1863-umc1460	*t*									6.0	3.1	3.2	7.2	5.4	1.0	2.4	4.7				
		t/*t*–1																				
Ph9	phi027-phi065	*t*																	4.4	4.0	4.5	6.1
		t/*t*–1																	2.4	1.1	4.0	6.3

a) Numbers following the two letters represent the chromosome locations of the QTL; b) *t* is the cumulative effects at time *t*, *t*/*t*–1 is the effects from time *t*–1 to *t*; c) additive effect; positive values of the additive effect indicate that the Zong3 alleles are in the direction of increasing the plant height; d) dominance effect; positive values of the dominance effect indicate that the heterozygotes have higher phenotypic values than the respective means of two homozygotes; e) log-likelihood value calculated by composite interval mapping; f) phenotypic variation explained by each QTL.

were detected in both locations. This indicated that the plant height QTL detected here showed no obvious interaction with environment, which is similar to some results in previous work[21,22]. This phenomenon could be explained by two possible reasons: (1) QTLs with strong effect rarely interact with environment because of their major effect, and the interactions between environment and QTL with weak effect were ignored due to the limitation of the statistical method[23]. (2) The plant height possesses a high hereditary capacity and is a little affected by environment.

The difference of the gene expression from $t-1$ to t could be revealed by the conditional analysis. Moreover, with the assistance of composite interval mapping, the developmental quantitative traits at a particular time could be dissected into Mendel's factors, and those factors could be located on chromosomes and their genetic effect could be evaluated. It is helpful to understand the time-space expression of QTL controlling plant heights. Analyses about the conditioned QTL and the unconditioned QTL in this study indicated that genes controlling plant heights in maize had an obvious dynamic characteristic. For example, although seven conditional QTLs were all detected in this study, any QTL could not be detected at all five testing stages, nor could seven QTLs be simultaneously detected at any particular testing stage. These results indicated that none of genes controlling plant heights could express throughout the entire growth process. It is consistent with theory of developmental genetics that gene expresses selectively at different developmental stages. Based on the phenotypic value in the final time, the effect of QTL controlling plant height was cumulative through entire developmental stages. The net effect of QTL controlling plant heights in special time could be estimated by the conditional QTL analysis method.

Marker assistant selection is one of the most important research directions in the molecular breeding. With the researches focused on molecular assistant selection of qualitative traits[24,25], however, there are only a few cases to apply molecular marker assistant selection to quantitative traits. It is because of hereditary complexity of the quantitative traits, which are controlled by the combination of many genes possessing the weak effect individually. This investigation also suggests that QTL mapping based on the analysis of final phenotypic value of a particular quantitative trait could not reveal the precise number and acting way of the genes controlling the trait. For example, Ph1-2 could not be detected in the final testing time, but could be found by both unconditional and conditional QTL analysis during the developmental progression. In another case of conditional QTL analysis, the new expression of Ph9 was detected in three testing times (Jun. 10, 13 and 16). Interestingly, the alleles from 87-1 increased phenotypic value during the first stage and the alleles from Zong3 increased the phenotypic value during the two other stages. Yan[11,13] observed similar phenomenon when they analyzed the dynamic developmental progression of the plant height and tiller number in rice. This indicated that the gene in a certain locus exhibits contrary genetic effect at the different developmental stages, and/or there are several genes controlling the same quantitative trait and expressing at different developmental stages so that QTL located dependent merely on the phenotypic value in the final time may lead to failure to detect these genes or the underestimation of their genetic values. Thus, QTL expressing at different phases should be considered, in addition to the interaction between QTL and environment, into, when marker assistant selection is performed.

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