Dynamic Mapping Based on Single Segment Substitution Lines for Plant Height in Rice

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1 Dynamic mapping based on single segment substitution lines for
2 plant height in rice

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1 **Abstract:**

2 **Background:** Dynamic regulations of QTLs still remain mysterious. Single segment substitution
3 lines and conditional QTL mapping, functional QTL mappings are ideal materials and methods to
4 explore epistatic interactions, expression patterns and functions of QTLs for complex traits.

5 **Results:** Based on single segment substitution lines five QTLs on plant height in rice were
6 identified first in this paper, and then their epistatic interactions, expression patterns and functions
7 were systematically studied by tailing after each QTL. Unconditional QTL mapping showed the
8 five QTLs were with significant effects at one or more stages, all of which increased plant height
9 except QTL₁. They interacted each other as homeostatic mechanisms to regulate plant height with
10 negative effects before 72d after transplanting and positive since then. Conditional QTL mapping
11 revealed the expression quantities and periods for the five QTLs and their epistases. Temporal
12 expression pattern was verified again by selective expressions of QTLs in specific periods. QTL₁
13 expressed negatively while QTL₂ and QTL₄ positively, mainly occurring in the periods from 35 to
14 42d and from 49 to 56d after transplanting. Epistatic expressions were dispersedly in various
15 periods, mainly with negative effects before 35d while positive since then. Functional QTL
16 mapping discovered the five QTLs brought the inflexion point ahead of schedule, accelerated the
17 growth and the degradation, and changed the peak of plant height, while their interactions had the
18 opposite effects approximately. This paper uncovered the dynamic rules of five QTLs and their
19 interactions on plant height systematically, which will be helpful to understand the genetic
20 mechanism for developmental traits.

21 **Conclusions:** Five single segment substitution lines were tested with significant additive,
22 dominant and epistatic effects of QTLs on plant height. Additive and dominant expressions were
23 mainly in two periods, while epistasis dispersedly. The five QTLs and their interactions
24 significantly regulated the developmental trajectory of plant height.

25 **Keywords:** Dynamics; Conditional QTL mapping; Functional QTL mapping; Epistasis; Single
26 segment substitution line; Plant height; Rice

27

1 Background

2 Plant type of rice, including root type, stem type, leaf type and spike type etc., is one of the
3 main factors to determine yield, and thus shaping of ideotype is an important way to improve rice
4 yield (Peng et al. 2008; Moles et al. 2009; Markel et al. 2020). Plant height is a crucial component
5 of plant type traits. On the one hand plant height is closely related to lodging resistance, plant
6 lodging during maturation surely resulting in the sharp decline of yield and quality of rice (Wang
7 et al. 2014). Development of dwarf and semi-dwarf rice cultivars has greatly increased the
8 capacity of lodging resistance and then the potentiality of yield since 1950s. On the other hand
9 plant height is a major determinant of plant's ability to compete for light because of the close
10 correlation with leaf number and leaf distribution, high stems being usually accompanied by high
11 biomass and then high grain yield (Falster and Westoby 2003; Wang and Li 2006). Given this
12 conflict ideotype suggests that suitable plant height should retain between 90cm and 120cm so as
13 to get the optimal output in cereal crop (Ren et al. 2016). Understanding the genetic basis of plant
14 height makes therefore it possible to find a balance between high yield and lodging. Specially,
15 plant height is one of relatively easily investigated traits, being able to be measured at a series of
16 stages to allow to dynamically explore the genetic mechanism of development. Thus plant height
17 is often used as one of model traits for the study of developmental behaviors (Yan et al. 1998b;
18 Cao et al. 2001; Yang et al. 2006).

19 QTL mapping is one of effective approaches to explore genetic mechanisms of quantitative
20 traits. For developmental traits like plant height, tiller number and leaf number etc., common QTL
21 mapping methods can be summarized as (1) unconditional mapping, (2) conditional mapping and
22 (3) functional mapping etc. (Xu and Zhu 2012). Unconditional QTL mapping usually analyzed
23 directly the phenotypic values measured at various growth stages, and then inferred the dynamic
24 genetic architecture of a developmental trait by longitudinal comparing of the mapping results
25 (Wu et al. 1999). Conditional QTL mapping needs to first estimate the conditional effects
26 $y(t|t-1)$ for the phenotypic values at time (t) given the phenotypes at time ($t-1$) (Zhu 1995;
27 Atchley and Zhu 1997), and then to conduct QTL mapping based on these estimations (Yan et al.
28 1998a, b; Wang et al. 1999; Cao et al. 2001). Conditional QTL mapping can effectively measure

1 the net expression of gene from time $(t-1)$ to time (t) since $y(t|t-1)$ is independent of $y(t-1)$
2 (the phenotypic value at time $(t-1)$) (Zhu 1999). Functional QTL mapping includes three steps,
3 fitting mathematical model for the development of a trait, estimating the parameters in the model
4 that defined the function, and then QTL mapping for these parameters (Ma et al. 2002; Cui et al.
5 2006, 2008; Wu et al. 2006). The advantage of functional QTL mapping is to detect QTLs that
6 regulated the shape and trajectory of trait changes owing to the incorporation of biological
7 principles (Wu et al. 2004). Studies via these strategies provided a wealth of information about
8 QTLs controlling developmental behavior of traits, such as QTL accumulated effects at a
9 point-in-time, QTL net effects in a period of time, and functional QTLs changed the process of
10 development etc. Over the past 30 years, great efforts have been made to dissect the genetic basis
11 of plant height (Yan et al. 1998b, Wang et al. 1999; Cao et al. 2001; Yang et al. 2006; Jiang et al.
12 2008; Zhu et al. 2015; Lei et al. 2018). Researches indicated that plant height in rice is generally
13 controlled by both qualitative and quantitative genes, more than 1000 QTLs having been mapped
14 on rice chromosomes, and their action mechanisms manifesting mainly accumulation and
15 interaction of QTL effects, i.e. additive effect and dominant or epistatic effect with the features of
16 spatio-temporal expression (<http://www.gramene.org/qlt>).

17 However, most of research materials applied in previous studies were conventional mapping
18 populations as F_2 self-pollinating populations (F_2), back-crossing populations (BC), double
19 haploid lines (DHLs), and recombinant inbred lines (RILs) etc., in which inconsistent genetic
20 backgrounds among individuals or lines could disturb the analysis results (Tanksley, 1993).
21 Moreover, systematical studies on developmental traits were rarely reported using various
22 approaches simultaneously, especially lacking to tail after the expression pattern for an identified
23 QTL. In this paper we applied five single segment substitution lines (SSSLs) as experimental
24 materials, to first identify whether carrying with putative QTLs on plant height for each SSSL, to
25 then estimate conditional effects $y(t|t-1)$ and four functional parameters in the
26 Wang-Lan-Ding's model, and to lastly carry out unconditional, conditional and functional QTL
27 mapping, respectively. Here the conditional effects were estimated based on phenotypic values of
28 plant height measured at nine time points of development. The Wang-Lan-Ding's model is about

the second-order ordinary differential equation of insect developmental rate with respect to temperature (Wang et al. 1982). The model, similar to the well known logistic model, was verified to be able to more accurately describe the entire developmental process of insects (Zhang and Tian 1995) and also can be applied to fit growth curve of developmental traits in crop (Liu et al. 2010a). We aimed to provide the first quantification of genetic patterns on plant height, including QTL effects and interactions, accumulated effects and net effects, as well as functions how to regulate the growth curve of plant height, and a comprehensive understanding of dynamic genetic mechanism for developmental traits as plant height.

Materials and methods

Materials and mapping population

The similar experimental materials as the previous study (Zhou et al. 2020), Huajingxian 74 (HJX74) and its five single segment substitution lines (SSSLs) (Table 1), were applied in this trial. HJX74 is an elite *indica* variety with many excellent properties cultured by our laboratory from South China. Each SSSL possessed only single substituted segment from a donor under HJX74 genetic background, distributing in related molecular marker regions on corresponding chromosomes with given lengths (Figure 1). Double segment substitution lines (DSSLs) were polymerized based on the F₂ populations from the crossing combinations of two SSSLs. A half diallel mating scheme was conducted using HJX74 and their SSSLs, DSSLs as crossing parents to generate the mapping population that included HJX74, 5 SSSLs, 7 DSSLs and 26 crossing combinations. Some of crossing combinations were lacking since the seeds of F₁ were scarce.

Field experiments and measurement of plant height

The same phenotypic trial as the previous study (Zhou et al. 2020) was applied in this study. The trial site located at the teaching and experimental station of South China Agricultural University, in Guangzhou, China (23°79'N, 113°159'E). In the early season (duration from March to July) of 2018, 39 genotypic materials were grown in a completely randomized block design with three replications. Germinated seeds were sowed in a seedling bed, and then seedlings

were transplanted to a rice field 20 days later with one plant per hill and the density of 16.7cm×16.7cm. Each plot consisted of four rows with ten plants per row. Local standard practices were used for the management of trail. Plant height per hill on 10 central plants were measured in each plot from seven days after transplanting onwards, and data every 7 days once was continuously recorded nine weeks (denoted by t_1 to t_9). The averages of plant height in each plot for the nine stages were used as input data for the subsequent analysis.

The Wang – Lan – Ding mathematical model

The phenotypic performance (y) of each plot during the nine measurement times (t) can be described by the equation (Wang et al. 1982):

$$y = \frac{K}{1 + \exp(-r(t - t_0))} \times (1 - \exp(-\frac{t - t_{\min}}{c})) \times (1 - \exp(-\frac{t_{\max} - t}{c}))$$

In the above model, the first term is a logistic model in which the parameter K is the upper limit of plant height, namely the potential maximum of plant height. t_0 is the inflexion point of the logistic curve, or the optimum time. r is the growth rate and c the degradation rate. The DUD (do not use derivatives) method was used to estimate all parameters in the model of the $(t_1, y_1), (t_2, y_2), \dots, (t_9, y_9)$ curve for each plot using SAS software v9.13. Then functional QTL mapping was conducted based on the estimations of the four parameters, respectively.

Statistical analysis and estimation of QTL effects

The model $y_{ij} = \mu + G_i + B_j + e_{ij}$ was adopted to analysis of variance on the phenotypic performance (y) of plant height measured for each plot at various stages, where μ, G, B and e were the estimations of population mean, genotype, block and residual error effect, respectively. And i, j represented serial numbers of genotypes and blocks, respectively. Additive effect (a) or dominant effect (d) of QTL was calculated by the estimations of $(S_i - HJX 74)$, and epistatic effect (e) between QTL pair by $(D_{ij} + HJX 74 - S_i - S_j)$. Where S and D indicated single and dual segment substitution materials respectively, and i, j represented two homozygotes or heterozygotes of SSSLs.

Conditional variable $y_{t|t-1}$ was estimated by the formula of $y_{t|t-1} = y_t - b_{t/t-1}(y_{t-1} - \bar{y}_{t-1})$, presenting phenotypic value at time t conditional on the phenotypic value at given time $t-1$, where y_{t-1} , $\bar{y}_{t-1}$ and y_t , $\bar{y}_t$ were the phenotypic values and the means at times $t-1$ and t , respectively. $b_{t/t-1}$ was the regression coefficient for phenotypic values at time t versus those at time $t-1$. QTL mapping was imposed on the conditional variable $y_{t|t-1}$ to generate conditional QTLs. Statistical analysis and estimation of QTL effects were carried out with `aov()` and `lm()` functions in R language (<https://www.r-project.org/>).

Results

Unconditional QTL mapping on plant height

Plant height approximately approached “S” type of growth curve (Figure 2). The figure drew from all 39 genotypic materials indicated that after slow, rapid growth plant height reached the peak and then started to decrease slightly. Separate analysis of variance at various stages revealed the significant difference of plant height existed among genotypes (Supplementary Table 1), supporting the existence of QTLs on plant height in the mapping population. The contrast tests found that each of the five SSSLs harbored plant height QTLs (Table 2). All carried with additive and/or dominant effects detected at one or more stages (see $QTL(t)$ in Table 2). QTL on SSSL S_5 (denoted by QTL_5 , similarly hereinafter) detected with significant dominant effects just at one of stages perhaps was unreliable. The other QTLs repeatedly appeared guaranteed the truth of them. Only did QTL_1 exhibited negative effects, the others showed to increase plant height. During the early period (from t_0 to t_3) few QTLs were detected, while more QTLs presented to the middle-late period. The variations of QTL effects with times implied the dynamics of expressions for these QTLs.

To understand the interaction mechanism among these QTLs, we first aggregated partly two of SSSLs to generate dual segment substitution line (DSSL) and then carried out a half diallel mating scheme to achieve various genotypes required so as to estimate epistasis. Four epistatic

1 components, additive-additive (aa), additive-dominance (ad), dominance-additive (da), and
2 dominance-dominance (dd), were estimated according to configurations of genotypes for seven
3 QTL pairs (Table 3). All seven pairs of S_i/S_j holding significantly interaction effects further
4 confirmed the prevalence of epistasis (see $QTL(t)$ in Table 3). Two epistatic components, d_1d_2
5 (denoted dd of S_1/S_2 , similarly hereinafter) and a_1a_5 were detected only at one of stages,
6 which reliability was subject to further verification. The other epistatic components were
7 significant at least at two stages, which indicated the validity of these interactions. Negative
8 epistatic effects were major, while positive epistases mainly appeared at the periods of t_8 and t_9 .
9 The causes of negative (positive) epistases perhaps were due to positive (negative) additive and
10 dominance effects of QTLs, which will be discussed later. All epistatic effects dynamically
11 changed with developmental stages (see $QTL(t)$ in Table 3).

12 **Conditional QTL mapping on plant height**

13 To acquire the net effect of a given QTL on plant height during a certain of period, we carried
14 out conditional QTL mapping. The conditional effects $y_{(t|t-1)}$, the net effects of phenotypic values
15 at time t given the phenotypic values at time $t-1$, were first estimated (Supplementary Table
16 2). And then conditional QTL effects, the net effects of QTLs from time $t-1$ to time t , were
17 calculated based on the conditional effects $y_{(t|t-1)}$ (see $QTL(t|t-1)$ in Table 2). Conditional
18 QTL revealed the quantities and the stages of QTL expressions. QTL₁ had twice expressions, one
19 was in the stage from t_5 to t_6 , exhibiting -6.57^{**} additive effect, and the other was from t_7 to
20 t_8 with -3.75^* additive effect and -4.96^{**} dominant effect. Similarly, QTL₄ expressed 3.39^*
21 dominant effect from t_3 to t_4 , 5.60^{**} additive effect and 3.82^* dominant effect from t_5 to t_6 ,
22 and QTL₂ 5.03^{**} dominant effect from t_8 to t_9 . Although QTL₂, QTL₃ and QTL₅ appeared
23 significant accumulated effects at certain of stages, the concentrated expression stages of these
24 QTLs were not detected due to without enough large expression quantities. There were not
25 significant expressions to be detected in the early period (from t_0 to t_3), QTL expressions

1 occurred mainly in the middle period (from t_3 to t_6) and the late period (from t_6 to t_9).

2 QTL interactions also exhibited different dynamic models (see $QTL(t|t-1)$ in Table 3).

3 In the early, middle and late periods, there were six, seven and thirteen significant epistatic
4 expressions, respectively. In the three periods, t_2-t_3 , t_4-t_5 and t_6-t_7 , QTLs hardly
5 expressed. There were 14 significant positive epistatic effects and 12 negative, respectively.
6 Mostly, negative expressions appeared in the early period, while positive in the late period. Some
7 of epistatic components had significant accumulated effects at certain of stages, but their
8 expression periods weren't detected due to dispersed expressing insignificantly. Inversely, some of
9 epistatic components had significant net effects in certain of stages, but didn't detect significant
10 accumulated effects due to reverse expressions. Lots of epistatic expressions were feeble so that
11 fail to be detected, while some large expressions became invisible for the reason of large error.

12

13 **Functional QTL mapping on plant height**

14 Functional QTL mapping is an appropriate method that passes a mathematical equation to
15 describe a biological developmental process with the genetic mapping framework (Ma et al. 2002).
16 We first applied the Wang-Lan-Ding model (Wang et al. 1982) to fit curves of plant height and to
17 estimate four functional parameters—the optimum time (t_0), the growth rate (r), the maximum
18 value (K) and the degradation rate (c) (Supplementary Table 3). And then based on these
19 estimations we carried out QTL mapping (Table 4). The five SSSLs were found to harbor QTLs
20 with additive and/or dominance to regulate the four parameters. Any one of SSSLs was associated
21 with two functional parameters at least, for which pleiotropy or close linkage of genes were
22 responsible. S_1 and S_5 involved in all of four parameters, and S_2 , S_3 and S_4 regulated t_0 or K
23 and c . For the parameter t_0 QTLs shortened the time of inflexion point on a curve. For r and
24 c , QTLs improved not only the growth rate but also the degradation rate. The impact of QTLs on
25 parameter K differed, enabling the potential of plant height to increase or decrease.

26 All pairs of S_i/S_j held interaction effects significantly, involving in one or more parameters by

1 various epistatic components. Interactions between QTL₂ and QTL₃, QTL₄, QTL₅ influenced one,
2 two and three parameters, respectively. While epistatic interactions between QTL₁ and the other
3 QTLs were associated with all of the four parameters. Epistases always regulated t_0 and K
4 positively, while r and c negatively (Table 4). The relationship that positive (negative)
5 epistasis were always derived from the interaction of negative (positive) QTLs was confirmed
6 once again.

7

1 Discussions

2 **Dynamic mapping for developmental traits**

3 Most traits of agricultural importance are under the control of an interacting network of genes,
4 which grow and develop through the dynamics of gene expressions during the whole growth
5 periods (Zhu 1995; Atchley and Zhu 1997). Studies via QTL mapping on different kinds of data
6 can provide a wealth of information about dynamics of QTLs regulating the developmental
7 behavior of quantitative traits (Xu and Zhu 2012). Unconditional QTL mapping on the direct
8 measured phenotypes at various developmental stages can detect the accumulated effects of QTLs
9 before a certain of static time point, but can't estimated the expression quantity due to the
10 correlations of phenotypes between two time points (Zhu 1995; Atchley and Zhu 1997).
11 Conditional QTL mapping on the indirect estimations of conditional phenotypes can provide net
12 expression of QTLs in a time interval and the stages of QTL expressions (Wang et al. 1999; Zhu
13 1999). And functional QTL mapping on the parameters defined in a mathematical function that
14 describes the trait variation with biological significance can reveal the QTLs regulating the shape
15 and the trajectory of developmental curve (Ma et al. 2002; Wu et al. 2004, 2006; Cui et al. 2006,
16 2008). In this paper we carried out systematical analysis for the dynamics of QTLs regulating the
17 developmental behavior of plant height in rice. We detected that the five SSSLs carried with
18 significant additive and/or dominant effects of QTLs on plant height at multiple developmental
19 stages. These QTLs were credible due to their repeatability of appearing. Except for QTL_1
20 exhibiting negative effects in the middle-late periods, the other QTLs showed the effects to
21 enhance plant height (see $QTL(t)$ in Table 2). These QTLs interacted each other to form genetic
22 network to regulate plant height. Seven pairs of SSSL combinations tested were all with one or
23 more significant epistatic components to mostly reduce plant height (see $QTL(t)$ in Table 3). QTLs
24 were characterized by temporal expression, selectively appearing significant effects in specific
25 stages of development. The five QTLs turned on mainly in the middle-late periods (see $QTL(t|t-I)$
26 in Table 2), whereas the seven QTL interactions dispersely in various periods (see $QTL(t|t-I)$ in
27 Table 3). Some expressions were too small to be statistically detected. Plant height varied
28 followed by the logistic curve of the Wang-Lan-Ding model approximately (Figure 1), which was

determined by the parameters of t_0 , r , K and c (Wang et al. 1982). These parameters changed the trajectory of growth curve of plant height including the inflection point, the growth rate, the peak value and the degradation rate. Our research indicated that the four functional parameters were regulated by the QTLs and the QTL interactions on the five SSSLs, each of which regulated two parameters at least (Table 4).

Dynamic patterns of QTL expressions

One of major goals in developmental genetics is to explore gene expression (Zhu 1995; Atchley and Zhu 1997). Conditional QTL mapping makes this possible, which can estimate the net expression of QTL in a certain of time interval (Wang et al. 1999; Zhu 1999). In theory, unconditional QTL effect at time point t is the accumulation effect of QTL from initial time to time t , which can be divided into several conditional QTL components, i.e. $QTL_t = QTL_1 + QTL_{2|1} + QTL_{3|2} + \dots + QTL_{t|t-1}$. Where conditional QTL effects were independent each other, and thus were additive. According to the formula, it is possible to generate following a few of cases at stage t , both QTL_t and $QTL_{t|t-1}$, either QTL_t or $QTL_{t|t-1}$, and neither QTL_t nor $QTL_{t|t-1}$ were significant. The relationship between unconditional QTLs and conditional QTLs was discussed in a our previous paper (Zhou et al. 2020) and was well validated by the results estimated in this paper. The correlation coefficient between QTL effects at the final stage t_9 and the sum of all conditional QTL effects before t_9 reached 0.9379** in the previous paper (Zhou et al. 2020) and 0.7208** in this paper, respectively(data not shown). Where only did a series of conditional QTLs truly reflected the expression periods and quantities of a QTL throughout the whole developmental stage. Conditional QTL mapping had widely been applied to reveal gene dynamic patterns for developmental traits (Yan et al. 1998a, b; Wang et al. 1999; Gao et al. 2001; Jiang et al. 2008; Liu et al. 2010b; Zhou et al. 2020). There were four representative patterns for the genetic control of growth trajectories, permanent QTLs, early QTLs, late QTLs and inverse QTLs (Wu et al. 2006). This knowledge derived from the accumulated effects of QTLs, QTLs being permanent, early, late and inverse when one genotype was better than

the other in entire growth process, at early stages, at late stages and one genotype showed inverse effects with the other since a particular stage, respectively. However, accumulated effects of QTLs couldn't reflect the expression stages and quantities of QTLs. This paper indicated that QTLs on plant height expressed all of additive, dominant and epistatic effects according to temporal expression pattern (see $QTL(t|t-I)$ in Table 2 and Table 3). QTLs and their interactions expressed significant effects only in one or more periods, and sometimes even hadn't significant expression periods while remained silent all the time. Permanent expression of QTLs was rare. QTL_1 and QTL_2 expressed mainly in the late period, QTL_4 in the middle period, while QTL_3 and QTL_5 were not detected significant expression periods (see $QTL(t|t-I)$ in Table 2). Similarly, QTL_1/QTL_2 , QTL_1/QTL_3 , QTL_1/QTL_5 and QTL_2/QTL_3 expressed mainly since the period t_5 , QTL_1/QTL_4 and QTL_2/QTL_4 dispersedly in various periods, and QTL_2/QTL_5 with inverse effects between the early period and the late period (see $QTL(t|t-I)$ in Table 3). In fact, QTLs and their interactions expressed net effects in various stages, just some of which reached the levels of significance statistically. Small expressions of QTLs were considered as no expressing or experimental error.

QTLs regulated developmental trajectories of temporal traits

Developmental theory considers if different genotypes at a given QTL correspond to different developmental trajectories, the QTL must affect the differentiation of this trait (Wu et al. 2006). Therefore, by estimating the functional parameters that define the trait curve of each QTL genotype and testing the differences in these parameters among genotypes, one can determine whether a QTL affects the formation and expression of a trait during development. In the Wang-Lan-Ding model, there were four parameters to regulate the growth curves of developmental traits, which might change the inflexion point (t_0), the upper limit (K), the rise speed (r) and the descent speed (c) of curves (Wang et al 1982). In this paper genotypes of five SSSLs differed from that of HJX74 at a given QTL (Figure 3), implying that a putative QTL existed on each of SSSLs. Both unconditional QTL mapping and conditional QTL mapping confirmed the existence of QTLs (Table 2). How did these QTLs affect the development of plant height? Functional QTL mapping based on the estimations of the four parameters indicated that

QTL₁ and QTL₅ regulated all of the four parameters by additive and/or dominant effects, and the other three QTLs influenced two of them, t_0 or K and c , respectively. These QTLs brought the inflexion point ahead of schedule, and accelerated the growth and the degradation of plant height. QTL₁ and QTL₅ made the maximum plant height shorter, while QTL₃ and QTL₄ higher (Table 4). Similarly, the interactions among these QTLs also influenced the four parameters, which always regulated t_0 and K positively, while r and c negatively by various epistatic components (Table 4).

Impact of epistasis on plant height

In multiple gene system, gene interaction is inevitable except for gene additive, which includes allelic interaction (dominance) and non-allelic interaction (epistasis) (Carlborg and Haley 2004; Wei et al. 2014). For statistical purpose, genotypic effect can be divided into single locus effects (the additive or the dominance) and interaction effects among segregating loci (the epistasis) (Mackay et al. 2009). Thus it can be seen that epistasis is one of important genetic components, a plausible feature of the genetic architecture of quantitative traits. Mapping epistatic interactions is challenging experimentally, statistically and computationally, which requires the large sample sizes, the severe penalty and the large number of tests (Mackay 2014). QTL mapping studies using primary mapping population such as F₂, BC, DHLs and RILs cannot clearly support the existence of specific interactions among QTLs because of the limitation of inconsistent genetic backgrounds among individuals or lines (Tanksley, 1993). SSSLs or NILs (near isogenic lines) have huge advantages for QTL identification in general and characterization of epistasis in particular (Tanksley, 1993; Eshed and Zamir, 1995, 1996). On the one hand target QTL can be detected by testing the difference between any one of SSSLs and the receptor parent; and on the other hand pyramiding of SSSLs enables estimation of epistatic effects (Lin et al. 2000; Chen et al. 2014; Qin et al. 2015; Zhu et al. 2015, 2018; Wang et al. 2018; Yang et al. 2018). In this paper we first detected the five SSSLs to carry with significant additive and/or dominant effects of QTLs on plant height (Table 2), and then four components of epistases were estimated via analysis of pyramiding materials derived from two SSSLs (Table 3). The information is reliable due to the

1 repeated emergence of putative QTLs and their interactions at multiple stages of development. All
 2 of seven pairs of SSSLs were tested with two or more significant effects of four epistatic
 3 components, further confirming the prevalence of epistasis (Table 3). Epistasis may be brought
 4 about by modification of gene function due to alterations in the signal-transducing pathway.
 5 Epistatic genes are more deleterious in combination than separately, which are often accompanied
 6 by inverse epistatic interactions as homeostatic (that is, canalizing) mechanisms (Mackay et al.
 7 2014). This role of epistasis was first observed by Eshed and Zamir (1996) when they found
 8 less-than-additive interactions between QTLs in tomato. We also confirmed inverse epistatic role
 9 on yield traits in rice that the negative epistasis derived mainly from the interactions between
 10 positive QTLs while the positive epistasis from negative QTLs (Wang et al. 2018; Zhou et al.
 11 2020). In this paper, most of QTLs were detected with positive additive and/or dominance, thus
 12 the estimations of epistatic components were mainly negative. Only after the stage of t_6
 13 occurred positive epistasis since negative QTLs appeared since then (Table 2 and Table 3). The
 14 property of epistasis was stipulated by the calculated formula $e_{ij} = g_{ij} - a_i - a_j$, where
 15 e , g , a indicated epistatic, genotypic and single locus effects respectively and i, j represented
 16 two loci. Because the value of e_{ij} is inversely proportional to the sum of single locus effects, it is
 17 more likely to gain negative (positive) epistasis when positive (negative) single locus effects.
 18 Additionally, one QTL always interacted with multiple other QTLs, forming genetic network. In
 19 this paper five QTLs were detected to interact each other with one or more significant epistatic
 20 components (Table 3). Of seven combinations of SSSLs set, QTL₁, QTL₂ interacted with the other
 21 four QTLs respectively, while QTL₃, QTL₄, QTL₅ at least with the other two QTLs. Five QTLs
 22 were with various interaction magnitudes, displaying different epistatic intensities. QTL₂ and
 23 QTL₄ seemed to be larger average epistatic effects and greater interoperability than the other
 24 QTLs (Supplementary Table 4). Of four epistatic components, average estimation of dd was
 25 seemingly larger than those of the others (Supplementary Table 4). Knowledge of epistatic
 26 interaction will improve our understanding of genetic networks and mechanisms that underlie
 27 genetic homeostasis, and improve predictions of response to artificial pyramiding breeding for
 28 quantitative traits in agricultural crop species. In the future, we must assess the effects of pairwise
 29 and higher order epistatic interactions between polymorphic DNA variants on molecular

interaction networks and, in turn, evaluate their effects on organismal phenotypes to understand the mechanistic basis of epistasis (Mackay et al. 2014). Only then will we be able to go beyond describing the phenomenon of epistasis to predicting and testing its consequences for genetic systems.

Conclusions

Based on single segment substitution lines we systematically analyzed dynamic regulations of five QTLs on plant height in rice. The five QTLs were with significant effects at one or more stages, all of which increased plant height except QTL₁. They interacted each other as homeostatic mechanisms to regulate plant height with negative effects before 72d after transplanting and positive since then. QTL₁ expressed negatively while QTL₂ and QTL₄ positively, mainly occurring in the periods from 35 to 42d and from 49 to 56d after transplanting. Epistatic expressions were dispersedly in various periods, mainly with negative effects before 35d while positive since then. The five QTLs brought the inflexion point ahead of schedule, accelerated the growth and the degradation, and changed the peak of plant height, while their interactions had the opposite effects approximately.

Abbreviations

HJX74: Huajingxian 74; HQTL: Quantitative trait locus; SSSL: Single segment substitution line; DSSL: Duple segment substitution line; F2: F1 self-pollinating populations; BC: Back-crossing population; DHL: Double haploid lines, and RIL: Recombinant inbred lines

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1 Authors' contributions

2 Y.F., H.Y.Z. and J.K.H. were the executives of trials and the writers, H.T.Z., X.L., S.H.B. and
3 Z.P.L. were the participators, L.J.M. was the cooperator, G.Q. Z. and S.K.W. were the leaders of
4 our research team, and G.F.L. was the constitutor of this study. All authors read and approved the
5 final manuscript.

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13 Availability of data and materials

14 The datasets supporting the conclusions of this article were included in this paper.

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16 Declarations

17 Ethics approval and consent to participate

18 This study complied with the ethical standards of China, where this research work was
19 conducted

20

21 Consent for publication

22 All authors provided their consent for publication.

23

1 Competing interests

2 The authors declare that they have no competing interests.

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1

2 Table 1 Single segment substitution lines (SSSLs) and their basic information. SSSL was the
 3 abbreviation of single segment substitution line. S_i represented the code of i th SSSL. Chr was the
 4 abbreviation of chromosome.

5

SSSL	Code	Chr	Marker on substituted segment	Donor parent
W23-03-08-09-27-82	S_1	3	End--PSM301-PSM304--RM569	Lemont
W08-18-09-09-06-02	S_2	6	RM549-RM136-RM527	IR64
W04-47-68-05-04-04-02-02	S_3	6	RM510--RM204--RM50--RM549	BG367
W06-26-35-01-05-02	S_4	8	PSM152--PSM154-RM72--RM404	Katy
W11-17-03-07-05-08	S_5	10	PSM166--RM596-RM271--RM269	Basmati 370

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2 Table 2 Additive and dominant effects of SSSLs on plant height at various developmental stages
 3 with the contrast of HJX74. SSSL was the abbreviation of single segment substitution line. S_i
 4 represented i th SSSL. a and d were additive and dominant effects, respectively, estimated by the
 5 mean of $S_i - HJX74$ (where i represented i th SSSL that was homozygote or heterozygote).
 6 QTL(t) and QTL($t|t-1$) represented unconditional and conditional QTL at stage t , respectively. t_i
 7 indicated various developmental stages, 7 days apart. Sign “-” meant to descend plant height due
 8 to the alleles from donors. Superscripts “*” and “**” indicated the significance at 5% and 1% level,
 9 respectively.

10

SSSL	Effect	QTL	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9
S_1	a	QTL(t)						-4.85*	-6.63**	-9.53**	-12.97*
		QTL($t t-1$)						-6.57**		-3.75**	
	d	QTL(t)								-6.55**	-7.71**
		QTL($t t-1$)								-4.96**	
S_2	a	QTL(t)				4.28*	4.40*	4.87*	4.14*		
		QTL($t t-1$)									
	d	QTL(t)				4.62*	4.45*				5.50*
		QTL($t t-1$)									5.03**
S_3	a	QTL(t)							4.97*	4.74*	6.50*
		QTL($t t-1$)									
S_4	a	QTL(t)						6.07**	6.92**	5.11*	5.83*
		QTL($t t-1$)						5.60**			
	d	QTL(t)		6.22*		6.87**	6.29**	6.83**	9.37**	5.77*	4.87*
		QTL($t t-1$)				3.39*		3.82*			
S_5	d	QTL(t)				5.19*					

$$\text{QTL}(t|t-1)$$

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2 Table 3 Epistatic effects between QTLs estimated on plant height at various developmental stages.

3 SSSL was the abbreviation of single segment substitution line. S_i represented i th SSSL. aa , ad ,4 da and dd were the abbreviations of epistatic components of additive-additive, additive-dominance,

5 dominance-additive and dominance-dominance, respectively, estimated by the mean of

6 $(D_{ij} + HJX74 - S_i - S_j)$ (where D_{ij} , S_i , S_j indicated dual segment and its two single segment7 materials respectively, which might be homozygotes or heterozygotes). $QTL(t)$ and $QTL(t|t-1)$ 8 represented unconditional and conditional QTL at stage t , respectively. t_i indicated various

9 developmental stages, 7 days apart. Sign “-” meant to descend plant height due to the alleles from

10 donors. Superscripts “*” and “**” indicated the significance at 5% and 1% level, respectively.

11

SSSL combination	Epistatic component	QTL	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9
S_1/S_2	ad	$QTL(t)$								8.21**	8.46**
		$QTL(t t-1)$						8.72**			
	dd	$QTL(t)$								7.80*	
		$QTL(t t-1)$						4.59*		5.96*	-5.82*
S_1/S_3	aa	$QTL(t)$				-9.78**	-9.01**				10.83**
		$QTL(t t-1)$									7.04**
	dd	$QTL(t)$									
		$QTL(t t-1)$								5.97*	-5.70*
S_1/S_4	ad	$QTL(t)$					-6.45*		-6.56*		
		$QTL(t t-1)$									5.17*
	da	$QTL(t)$		6.67*							7.48*
		$QTL(t t-1)$		6.10*						6.45*	
	dd	$QTL(t)$				-8.74**	-11.37**	-4.35*	-7.20*		
		$QTL(t t-1)$				-6.37*				5.26*	
S_1/S_5	aa	$QTL(t)$									8.58**

		QTL($t t-I$)								6.26 [*]
	<i>da</i>	QTL(t)							8.04 ^{**}	7.28 [*]
		QTL($t t-I$)							8.37 ^{**}	
	<i>dd</i>	QTL(t)								
		QTL($t t-I$)							6.31 [*]	
S_2/S_3	<i>aa</i>	QTL(t)	-7.76 [*]	-7.33 [*]	-8.75 ^{**}	-6.66 [*]	-7.70 [*]			
		QTL($t t-I$)					-4.50 [*]			
S_2/S_4	<i>aa</i>	QTL(t)		-7.61 [*]	-7.76 [*]		-6.97 [*]			
		QTL($t t-I$)					-4.12 [*]			
	<i>ad</i>	QTL(t)	-9.29 ^{**}		-11.17 ^{**}	-10.77 ^{**}	-8.26 ^{**}	-10.25 ^{**}		
		QTL($t t-I$)			-5.65 [*]				5.21 [*]	
	<i>dd</i>	QTL(t)	-10.96 ^{**}	-12.21 ^{**}	-9.67 ^{**}	-15.07 ^{**}	-14.47 ^{**}	-8.18 [*]	-9.97 ^{**}	-9.28 [*]
		QTL($t t-I$)	-10.96 ^{**}	-6.19 [*]		-6.36 [*]				
S_2/S_5	<i>ad</i>	QTL(t)	-12.02 ^{**}	-13.03 ^{**}	-9.56 ^{**}	-8.77 ^{**}	-8.13 ^{**}	-7.87 [*]		
		QTL($t t-I$)	-12.02 ^{**}	-6.43 [*]					6.14 [*]	
	<i>dd</i>	QTL(t)	-14.16 ^{**}	-11.71 ^{**}	-9.40 ^{**}	-11.66 ^{**}	-8.37 ^{**}			
		QTL($t t-I$)	-14.16 ^{**}							

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1 Table 4 QTL effects for the four functional parameters on plant height. SSSL was the abbreviation
2 of single segment substitution line. S_i represented the homozygote or heterozygote of i th SSSL.
3 Additive effect (a) or dominant effect (d) of QTL was estimated by the mean of $(S_i - HJX74)$,
4 where HJX74 was the abbreviation of Huajingxian 74. aa , ad , da and dd represented the
5 additive-additive, additive-dominance, dominance-additive and dominance-dominance epistatic
6 components, respectively, which were estimated by the mean of $(D_{ij} + HJX74 - S_i - S_j)$ (where
7 D_{ij} , S_i , S_j indicated dual segment and its two single segment materials respectively, which
8 might be homozygotes or heterozygotes). t_0 , r , K and c were the optimum time, the growth
9 rate, the maximum value and the degradation rate, respectively. Sign “-” meant to descend the
10 parameters due to the alleles from donors. Superscripts “*” and “**” indicated the significance at 5%
11 and 1% level, respectively.

12

SSSL or their combination	Effect	t_0	r	K	c
S ₁	a	-1.16**	0.16**	-16.72**	0.27**
	d	-0.46*		-12.71**	0.25**
S ₂	d	-0.42*			0.18**
S ₃	a			6.49*	0.28**
	d				0.27**
S ₄	a			5.82*	0.22**
	d			4.77*	
S ₅	a	-0.46*		-6.11*	
	d	-0.45*	0.09**	-4.47*	0.18**
S ₁ /S ₂	aa	0.80*	-0.13**	4.19	
	ad	1.33**		9.55*	-0.45**
	da			9.62*	-0.23**
	dd			7.95*	-0.22**

S ₁ /S ₃	<i>aa</i>	1.77 ^{**}	-0.16 ^{**}	18.38 ^{**}	-0.26 ^{**}
	<i>ad</i>	0.79 [*]	-0.21 ^{**}		-0.39 ^{**}
	<i>da</i>				-0.32 ^{**}
	<i>dd</i>				-0.52 ^{**}
S ₁ /S ₄	<i>aa</i>	0.79 [*]	-0.18 ^{**}	8.76 [*]	-0.25 ^{**}
	<i>ad</i>	0.57 [*]			
	<i>da</i>				-0.47 ^{**}
	<i>dd</i>		-0.09 [*]		-0.15 [*]
S ₁ /S ₅	<i>aa</i>	1.03 ^{**}	-0.09 [*]	8.52 [*]	-0.26 ^{**}
	<i>ad</i>	0.72 [*]	-0.08 [*]		-0.19 ^{**}
	<i>da</i>		-0.09 [*]	16.78 ^{**}	-0.23 ^{**}
	<i>dd</i>		-0.13 ^{**}	10.39 [*]	-0.15 [*]
S ₂ /S ₃	<i>aa</i>	0.59 [*]			-0.28 ^{**}
	<i>ad</i>	0.58 [*]			-0.28 ^{**}
	<i>da</i>				-0.26 ^{**}
	<i>dd</i>				-0.45 ^{**}
S ₂ /S ₄	<i>aa</i>	0.63 [*]			-0.23 ^{**}
	<i>ad</i>	0.70 [*]			
	<i>da</i>	0.60 [*]			-0.41 ^{**}
	<i>dd</i>	0.91 ^{**}			
S ₂ /S ₅	<i>aa</i>			8.66 [*]	0.27 ^{**}
	<i>ad</i>	0.88 ^{**}			
	<i>da</i>	0.97 ^{**}		10.23 [*]	
	<i>dd</i>	1.15 ^{**}			-0.17 ^{**}

1

2 Figure Legend

3 Figure 1 The approximate lengths and locations of substitution segments on chromosomes. Chr
4 was the abbreviation of chromosome, which was followed by chromosomal number. Genetic
5 distance (cM) and marker codes were listed on the left and the right of Chr, respectively. The
6 vertical lines on the right of Chr represented substitution segments with serial number S_i .

7

8 Figure 2 The growth curves of 39 genotypes for plant height over time. ti represented i th stage
9 measured, interval of 7 days. Unit of plant height was in cm.

10

11 Figure 3 Different trajectories corresponding to different genotypes at a given QTL. S_0
12 represented the genotype (aa) of HJX74, while S_i and H_i indicated the genotypes (AA and Aa)
13 of i th single segment substitution line. ti indicated various developmental stages, the difference of
14 7d. Unit of plant height was in cm.

15

Figures

Figure 1

The approximate lengths and locations of substitution segments on chromosomes. Chr was the abbreviation of chromosome, which was followed by chromosomal number. Genetic distance (cM) and marker codes were listed on the left and the right of Chr, respectively. The vertical lines on the right of Chr represented substitution segments with serial number Si.

Figure 2

The growth curves of 39 genotypes for plant height over time. t_i represented i th stage measured, interval of 7 days. Unit of plant height was in cm.

Figure 3

Different trajectories corresponding to different genotypes at a given QTL. S₀ represented the genotype (aa) of HJX74, while S_i and H_i indicated the genotypes (AA and Aa) of *i*th single segment substitution line. *i* indicated various developmental stages, the difference of 7d. Unit of plant height was in cm.

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