CROP BREEDING AND APPLIED BIOTECHNOLOGY

ARTICLE

Control of plant height by 24 alleles at 12 quantitative trait loci in rice

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Abstract: *Plant height (PH) is controlled by quantitative trait loci (QTLs) in rice. In the present study, a recombinant inbred line population developed by crossing two rice cultivars, Lemont and Yangdao4, was grown in eight environments for QTL analysis. Multiple interval mapping detected 53 PH-QTLs, 39 of which clustered at 12 chromosome regions/putative loci. An examination of the 12 putative loci identified 24 alleles that are simultaneously involved in controlling PH. Linear regression analyses suggested that these 24 alleles function additively across the 12 loci to control PH, and plants carrying more PH-increasing alleles at the 12 loci were taller than those carrying more PH-decreasing alleles. Multiple comparison tests indicated that the effect of a single allele at the 12 loci was small and that multiple alleles must be pyramided to attain a statistically significant effect. The closest markers to the 12 loci can be used directly in marker-assisted breeding to manipulate PH.*

Keywords: *rice, plant height, QTL, allele, recombinant inbred line*

INTRODUCTION

In rice (*Oryza sativa* L.) production, the occurrence of lodging is common during the grain fill period after strong winds accompanied by heavy rain (Sowadan et al. 2018). Lodging reduces the yield, quality of produce, and mechanical harvesting efficiency (Weber and Fehr 1966, Sowadan et al. 2018). Plant height (PH), an important trait affecting lodging, has been the primary target for improving resistance against lodging (Sowadan et al. 2018). During the 1960s, rice varieties with reduced PH (semidwarf varieties) and improved lodging resistance were developed that strongly increased the rice yield and initiated the rice green revolution in Asia (Khush 1999).

Rice PH is controlled by quantitative trait loci (QTLs) (Huang et al. 1996). Thousands of QTLs for PH have been mapped on all 12 rice chromosomes using QTL analysis (Li et al. 1995, Huang et al. 1996, Feng et al. 2011, Wen et al. 2015, Han et al. 2017) or association mapping (Zhou et al. 2016, Sowadan et al. 2018). Genes controlling rice PH have been characterized or cloned, including 17 genes involved in the gibberellin pathways, 25 genes involved in the brassinosteroid pathways, 10 genes involved in the strigolactone pathways, and 22 genes involved in other phytohormone pathways (Liu et al. 2018). The famous green revolution gene *sd1* was cloned and characterized by three independent groups in 2002 (Monna et al. 2002, Sasaki et al. 2002, Spielmeyer et al. 2002).

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Recombinant inbred line (RIL) populations are often used to detect and confirm PH-QTLs. Although QTLs related to PH have been identified using different RIL populations, it is still largely unknown how the different QTLs detected within a specific population control PH and whether these QTLs can be used simultaneously to manipulate PH. In this study, we used a RIL population developed by crossing two rice cultivars, Lemont and Yangdao4. The objectives were to use the Lemont ´ Yangdao4 RIL population to (1) detect QTLs related to PH, (2) examine how the combination of different alleles in different QTLs determines PH, and (3) explore molecular markers that can be used to manipulate PH.

MATERIAL AND METHODS

RIL population

The present study used a rice RIL population consisting of 219 lines developed via single seed descent by crossing Lemont, an American *japonica* variety, with Yangdao4, a Chinese *indica* variety. The Lemont ´ Yangdao4 RIL population was initially developed for mapping sheath blight resistance QTLs.

The RIL population was sown in eight different environments on the farm of the China National Rice Research Institute (CNRRI) in Fuyang (lat 119° 95' E, long 30° 07' N), Hangzhou, or the CNRRI trial station in Lingshui (lat 110° 02' E, long 18° 48' N), Hainan, for QTL analysis: (1) May 24, 2013, in Hangzhou; (2) November 23, 2016, in Hainan; (3) May 29, 2017, in Hangzhou; (4) June 7, 2017, in Hangzhou; (5) June 30, 2017, in Hangzhou; (6) November 25, 2017, in Hainan; (7) May 23, 2018, in Hangzhou; and (8) June 2, 2018, in Hangzhou.

Measurement of PH

The 219 lines of the RIL population were planted as 219 plots in eight different environments as mentioned above for measurement of PH. Plot locations were randomized. Eighteen individual plants of each line were planted in every environment. The 18 plants were arranged in three rows of six plants each, separated by 20 cm between rows and 17 cm between the plants of each row. Five plants of each line were randomly selected for measurement of PH, which was measured from the soil surface to the tip of the tallest panicle (not including awn). The average PH of five plants of each line was used for QTL analysis.

Construction of genetic linkage map

A total of 208 polymorphic markers covering the 12 rice chromosomes were used to construct a genetic linkage map using Mapmaker/EXP version 3.0 (Lander et al. 1987). The 208 polymorphic markers consisted of insertion-deletion markers with 'D' or 'G' prefix and simple sequence repeat markers with 'RM' prefix. The names of the 208 markers are provided in Figure 1 and Figure 2. The primer sequences of the insertion-deletion 'D' markers have been reported by Zeng et al. (2013). The sequences of the simple sequence repeat 'RM' markers can be found at the Gramene website (www.gramene.org). The sequences of the insertion-deletion 'G' markers are as follows: GW1C (5'-AGCGTTCGCAACTTCG-3', 5'-ATCCGTTCCGCTTCCA-3'), GL31C (5'-ATGGTCGGAGTTGTGGAAGTG-3',5'-CATCGGTGCATCGTGGG-3'), GL31F (5'-CTGCACGGAGCGCATAGA-3', 5'-TTGGAGTGGTTGGGAGACG-3'), GW32F (5'-TGACTCCACCAGAACC-3',5'-AAACCCAAACACGAAT-3'), GL32G (5'-CTGCGATTGTATCTCACTT-3', 5'-CTCATGGAGGACAGAAGA-3'), GL4F (5'-GAACAGCGTGTATTGGT-3', 5'-GAGGGAAGAAGAGGAAA-3'), and GL4J (5'-TACCGTTCGAGTAAACCC-3', 5'-CTGCTTCCCTTGTGCTT-3').

A genetic linkage map was constructed using 208 polymorphic markers to assay leaves of the 219 lines of the Lemont ´ Yangdao4 RIL population. DNA extraction and PCR protocol followed Ye et al. (2017).

Multiple interval mapping and statistical analysis

Multiple interval mapping (MIM) was run in Windows QTL Cartographer 2.5 software (Wang et al. 2012). The MIM model used for QTL analysis followed Zeng et al. (2016). Detection of two or more QTLs in the same marker interval was defined as a QTL cluster. The statistical analysis, including linear regression analysis and Duncan's multiple range test, was performed using SAS 8.01 software (SAS Institute, Cary, NC, USA).

RESULTS AND DISCUSSION

QTLs identified using the MIM method

A genetic linkage map was constructed with 208 polymorphic markers covering 12 rice chromosomes. The linkage map represented a total of 2228.0 cM with an average of 11.4 cM between adjacent markers (Figures 1 and 2).

QTL analysis detected a total of 53 PH-QTLs in eight environments using MIM (Figures 1 and 2). These QTLs are mapped on 10 of the 12 chromosomes. Forty-eight of the 53 QTLs accounted for less than 10% of the phenotypic variation individually, indicating that most of the QTLs had a minor effect. Five of the 53 QTLs had a relatively large effect that accounted individually for 12.9–15.2% of the phenotypic variation: *qPH10.2* (detected in 2016 in Hainan), *qPH2.2* (detected on May 29, 2017, in Hangzhou), *qPH12.3* (detected on June 7, 2017, in Hangzhou), *qPH12.1* (detected on June 30, 2017, in Hangzhou), and *qPH12.1* (detected on June 2, 2018, in Hangzhou) accounted for 13.0%, 12.9%, 15.2%, 13.0%, and 12.9% of the phenotypic variations, respectively.

It was found that most of the QTLs were clustered in some QTL-rich regions: thirty-nine QTLs were clustered in twelve QTL-rich regions (Table 1). We focused on the 12 QTL clusters/putative loci because a QTL cluster consists of at least two QTLs and is expected to be more stable than a QTL detected only once.

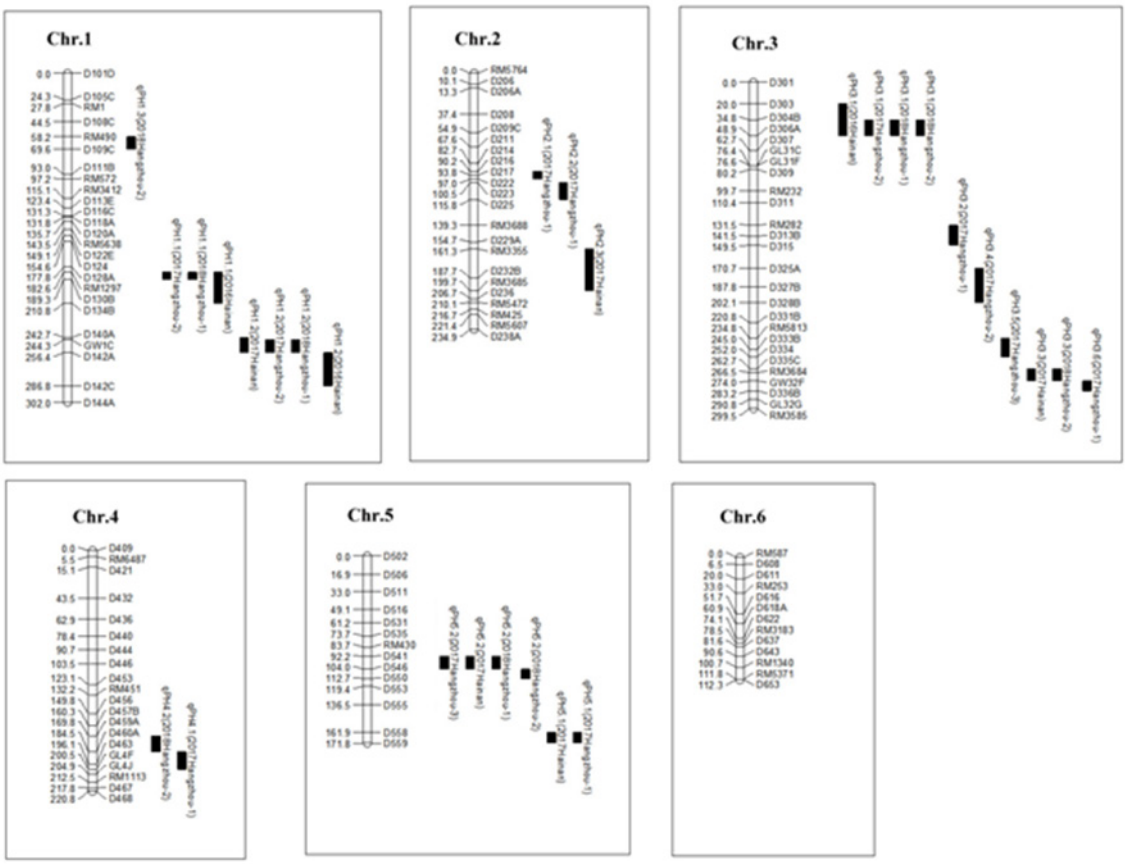

Figure 1. Genetic linkage map (chromosomes 1–6) constructed using the Lemont´Yangdao4 recombinant inbred line population consisting of 219 lines and QTLs responsible for plant height detected using multiple interval mapping in eight environments. The environments are listed in parentheses after the QTL name at the right of the chromosome bars. 2017 Hangzhou-1: sown in May 29, 2017, in Hangzhou; 2017 Hangzhou-2: sown in June 7, 2017, in Hangzhou; 2017 Hangzhou-3: sown in June 30, 2017, in Hangzhou; 2018 Hangzhou-1: sown in May 23, 2018, in Hangzhou; and 2018 Hangzhou-2: sown in June 2, 2018, in Hangzhou.

Control of PH by 24 alleles at 12 putative loci

We examined all 12 putative loci carefully. At five putative loci (*qPH1.2*, *qPH3.3*, *qPH8.2*, *qPH9.1*, and *qPH10.2*), the alleles for increased height were from Lemont; at the other seven loci (*qPH1.1*, *qPH3.1*, *qPH5.2*, *qPH5.1*, *qPH11.1*, *qPH12.1*, and *qPH12.3*), the alleles for increased height were from Yangdao4 (Table 1). The 12 PH-increasing alleles were *qPH1.2LE*,

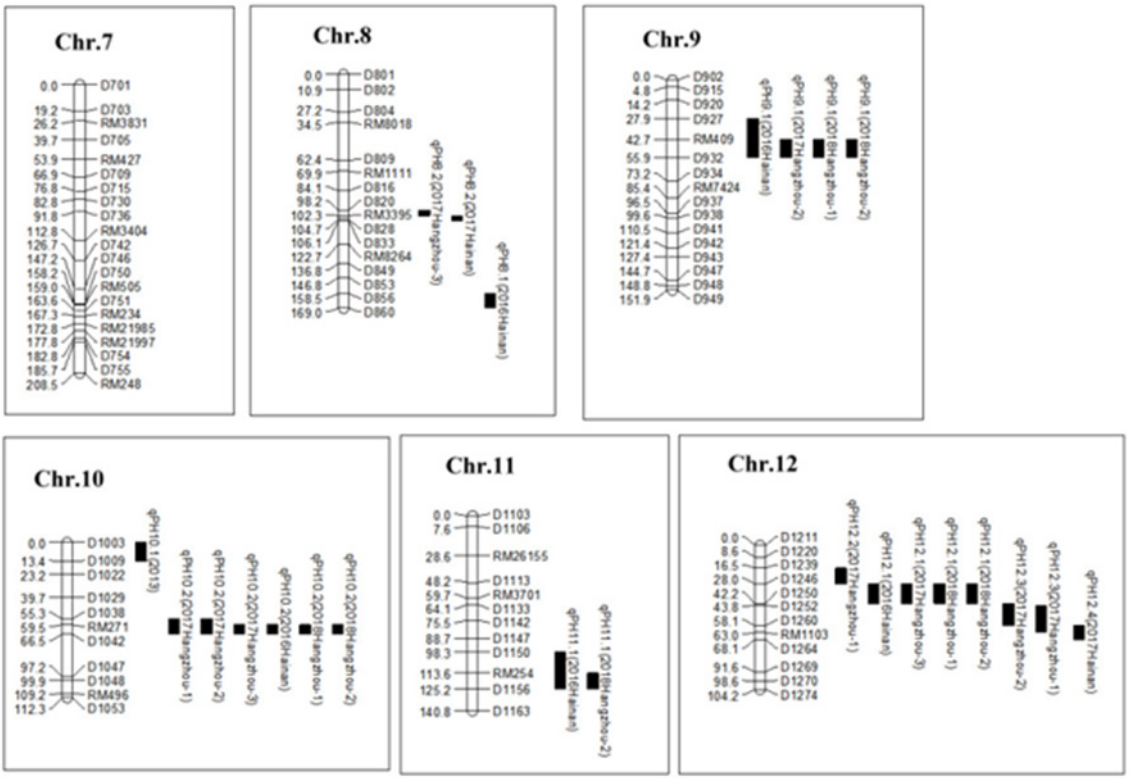

Figure 2. Genetic linkage map (chromosomes 7–12) constructed using the Lemont´Yangdao4 recombinant inbred line mapping population consisting of 219 lines and QTLs responsible for plant height detected using multiple interval mapping in eight environments. The environments are listed in parentheses after the QTL name at the right of the chromosome bars. 2017 Hangzhou-1: sown in May 29, 2017, in Hangzhou; 2017 Hangzhou-2: sown in June 7, 2017, in Hangzhou; 2017 Hangzhou-3: sown in June 30, 2017, in Hangzhou; 2018 Hangzhou-1: sown in May 23, 2018, in Hangzhou; and 2018 Hangzhou-2: sown in June 2, 2018, in Hangzhou.

Table 1. Thirty-nine plant height QTLs identified by multiple interval mapping were clustered in twelve QTL-rich regions/putative loci

Chr.	Name of putative loci	No. of collocated QTLs detected at the QTL cluster	Marker interval	Nearest marker	Additive effect[a]	R^2(%) for collocated QTLs detected at the QTL cluster
1	*qPH1.1*	3	RM1297-D134B	D130B	-	4.4, 9.1, 3.0
1	*qPH1.2*	4	D140A-D142C	D142A	+	7.8, 3.6, 8.3, 2.8
3	*qPH3.1*	4	D303-D306A	D304B or D306A	-	8.2, 7.3, 8.1, 5.6
3	*qPH3.3*	2	D335C-GW32F	RM3684	+	6.4, 4.3
5	*qPH5.2*	4	D541-D550	D546	-	7.4, 8.6, 6.9, 5.2
5	*qPH5.1*	2	D558-D559	D559	-	4.7, 3.7
8	*qPH8.2*	2	D820-D833	RM3395 or D828	+	4.4, 5.1
9	*qPH9.1*	4	D927-D932	RM409 or D932	+	2.8, 6.5, 3.1, 1.5
10	*qPH10.2*	6	D1038-D1042	RM271 or D1042	+	13, 4, 2.3, 3.6, 5.5, 4.6
11	*qPH11.1*	2	D1150-D1156	RM254	-	4.3, 2.7
12	*qPH12.1*	4	D1246-D1252	D1250	-	9.8, 13, 8.4, 12.9
12	*qPH12.3*	2	D1250-RM1103	D1252 or D1260	-	15.2, 5.7

[a]A negative additive effect (-) indicated that the allele from Yangdao4 increased plant height, whereas a positive additive effect (+) indicated that the allele from Lemont increased plant height.

qPH3.3LE, *qPH8.2LE*, *qPH9.1LE*, *qPH10.2LE*, *qPH1.1YD*, *qPH3.1YD*, *qPH5.2YD*, *qPH5.1YD*, *qPH11.1YD*, *qPH12.1YD*, and *qPH12.3YD,* and the 12 PH-decreasing alleles were *qPH1.2YD*, *qPH3.3YD*, *qPH8.2YD*, *qPH9.1YD*, *qPH10.2YD*, *qPH1.1LE*, *qPH3.1LE*, *qPH5.2LE*, *qPH5.1LE*, *qPH11.1LE*, *qPH12.1LE*, and *qPH12.3LE*; 'LE' or 'YD' suffixes in QTL names indicate if it was inherited from 'Lemont' or 'Yangdao4', respectively.

First, we calculated how many PH-increasing alleles and PH-decreasing alleles existed at the 12 putative loci for different lines of the Lemont ´ Yangdao4 RIL population. The nearest markers to each of the 12 loci were selected to represent the 12 loci (Table 1). The 12 markers are D130B, D142A, D306A, RM3684, D546, D559, RM3395, RM409, RM271, RM254, D1250, and D1260. Second, we used regression analysis to test in the RIL population whether more PH-increasing alleles in a line would lead to a taller PH phenotype. Regression analysis using data in eight environments proved this assumption and yielded eight equations (May 2013, Hangzhou: F= 13.2, $P = 0.0004$; November 2016, Hainan: F = 92.0, $P< 0.0001$; May 29, 2017, Hangzhou: F = 74.2, $P< 0.0001$; June 7, 2017, Hangzhou: F = 86.5, $P < 0.0001$; June 30, 2017, Hangzhou: F = 123.6, $P< 0.0001$; November 2017, Hainan: F = 76.0, $P< 0.0001$; May 23, 2018, Hangzhou: F = 105.9, $P < 0.0001$; and June 2, 2018, Hangzhou: F = 96.6, $P< 0.0001$). The eight equations are provided in Figure 3 and Figure 4. These results indicated that (1) plants carrying more height-increasing alleles at the 12 loci were taller than those carrying more height-decreasing alleles and (2) PH was controlled at least by the 12 loci simultaneously.

Effect of a single allele at the 12 putative loci

There are 24 alleles at the 12 putative loci. We examined the extent of the effect of a single allele on the PH phenotype by using the following method. First, we classified the different lines of the RIL population into 8 different groups based on the number of height-increasing alleles each carried at the 12 putative loci (Figures 5 and 6). However, because of the limited number of lines within the RIL population, lines with more than 20 height-increasing alleles or less than 6 cannot be found. Second, we used Duncan's multiple range test ($P = 0.05$) to compare the differences among the 8 different groups (Figures 5 and 6). The analysis showed that lines carrying 6, 8, or 10 height-increasing alleles did not significantly differ in PH among the 8 environments. Plants carrying 12 or 14 height-increasing alleles did not have a significantly

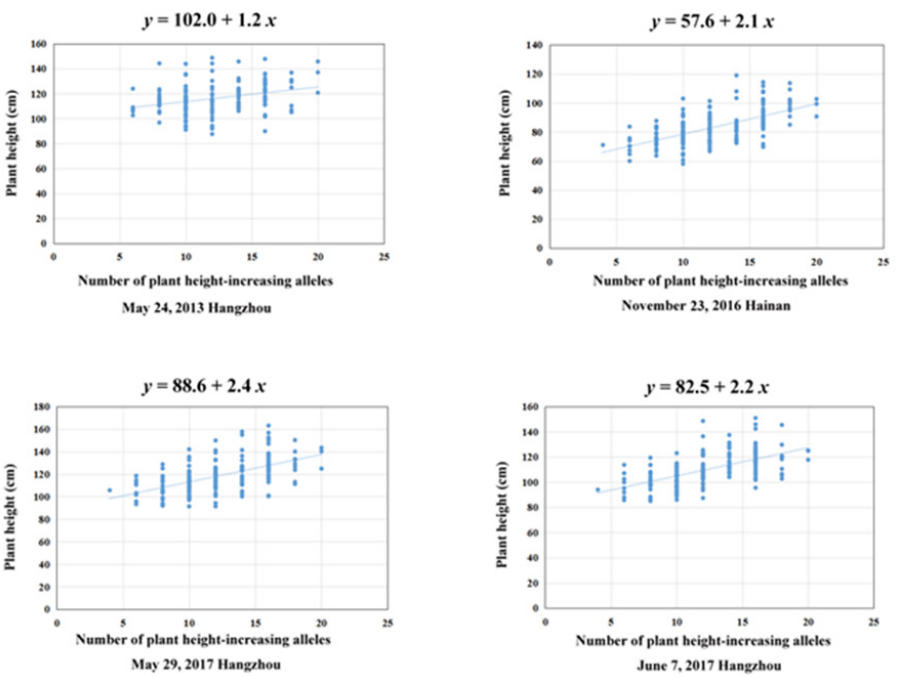

Figure 3. Regression analysis between plant height and number of plant height-increasing alleles at 12 loci (*qPH1.1*, *qPH1.2*, *qPH3.1*, *qPH3.3*, *qPH5.2*, *qPH5.1*, *qPH8.2*, *qPH9.1*, *qPH10.2, PH11.1*, *qPH12.1*, and *qPH12.3*) using 219 lines of the Lemont ´ Yangdao4 RIL population planted in four environments: (1) sown on May 24, 2013, in Hangzhou; (2) sown on November 23, 2016, in Hainan; (3) sown on May 29, 2017, in Hangzhou; and (4) sown on June 7, 2017, in Hangzhou.

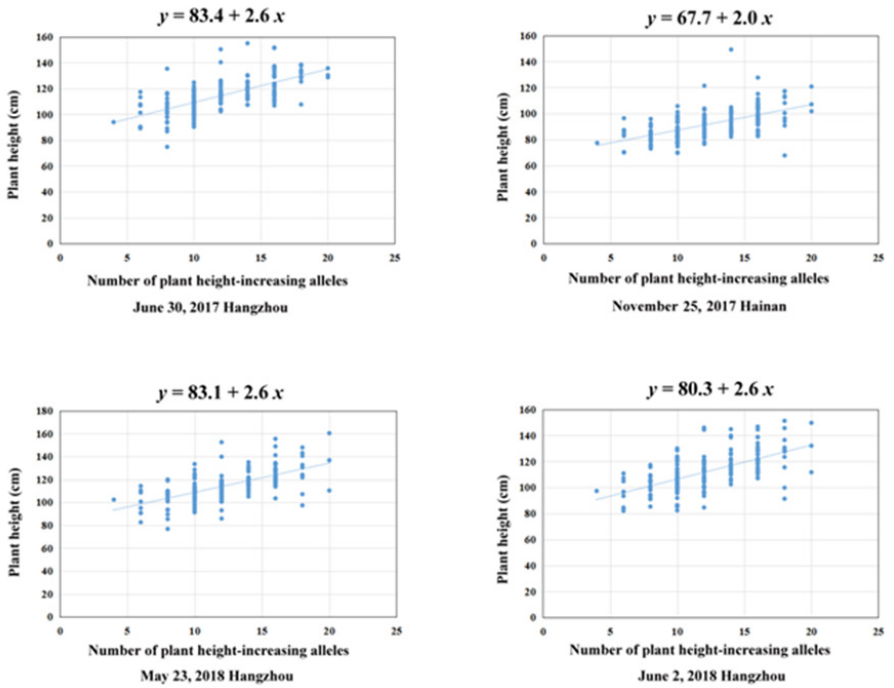

Figure 4. Regression analysis between plant height and number of plant height-increasing alleles at 12 loci (*qPH1.1*, *qPH1.2*, *qPH3.1*, *qPH3.3*, *qPH5.2*, *qPH5.1*, *qPH8.2*, *qPH9.1*, *qPH10.2, PH11.1*, *qPH12.1*, and *qPH12.3*) using 219 lines of the Lemont ´ Yangdao4 RIL population planted in four environments: (1) sown in June 30, 2017, in Hangzhou; (2) sown in November 25, 2017, in Hainan; (3) sown in May 23, 2018, in Hangzhou; and (4) sown in June 2, 2018, in Hangzhou.

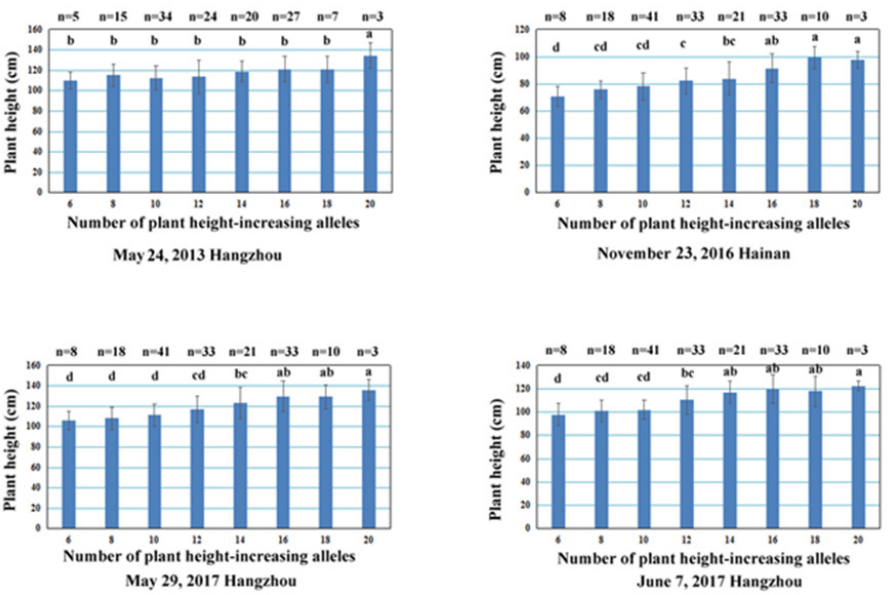

Figure 5. Multiple comparison test (Duncan's, *P* = 0.05) among different lines carrying different numbers of plant height-increasing alleles at the Lemont´Yangdao4 recombinant inbred line population planted in four different environments: (1) sown on May 24, 2013, in Hangzhou; (2) sown on November 23, 2016, in Hainan; (3) sown on May 29, 2017, in Hangzhou; and (4) sown on June 7, 2017, in Hangzhou. Different lines of the Lemont´Yangdao4 RIL population were classified into 8 different groups based on the number of height-increasing alleles that they carried at 12 loci (*qPH1.1*, *qPH1.2*, *qPH3.1*, *qPH3.3*, *qPH5.2*, *qPH5.1*, *qPH8.2*, *qPH9.1*, *qPH10.2, PH11.1*, *qPH12.1*, and *qPH12.3*).

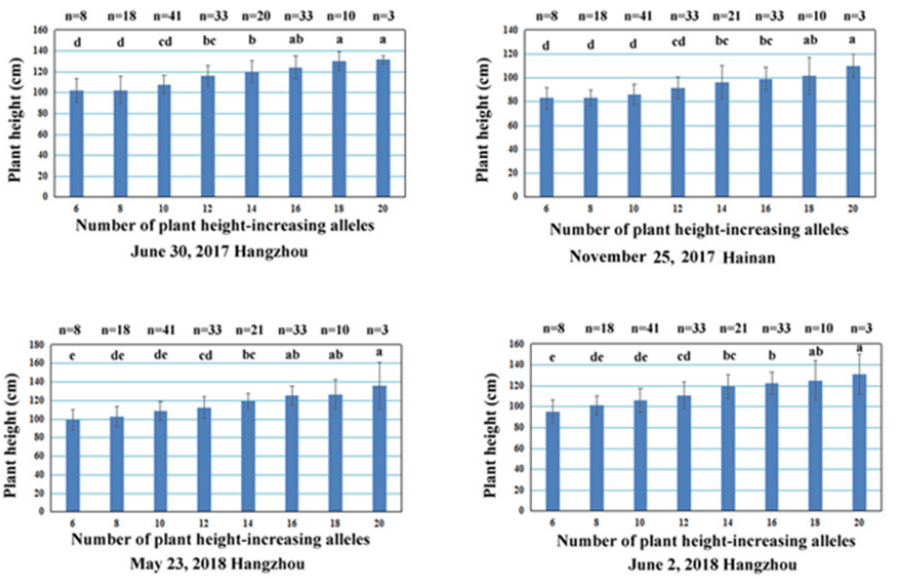

Figure 6. Multiple comparison test (Duncan's, $P = 0.05$) among different lines carrying different numbers of plant height-increasing alleles at the Lemont´Yangdao4 recombinant inbred line population planted in four different environments: (1) sown in June 30, 2017, in Hangzhou; (2) sown in November 25, 2017, in Hainan; (3) sown in May 23, 2018, in Hangzhou; and (4) sown in June 2, 2018, in Hangzhou. Different lines of the Lemont´Yangdao4 RIL population were classified into 8 different groups based on the number of height-increasing alleles that they carried at 12 loci (*qPH1.1*, *qPH1.2*, *qPH3.1*, *qPH3.3*, *qPH5.2*, *qPH5.1*, *qPH8.2*, *qPH9.1*, *qPH10.2, PH11.1*, *qPH12.1*, and *qPH12.3*).

different PH. Similarly, plants carrying 14 or 16 height-increasing alleles did not have a significantly different PH (Figure 5 and 6). These observations indicated that the contribution of each of the 24 alleles at the 12 loci was incremental, one or several alleles at the 12 loci cannot achieve a significant contribution to the final PH phenotype. This finding was consistent with the MIM mapping results that most of the identified QTLs had only a minor effect. Therefore, if the 12 loci would be used in marker-assisted selection, we suggest that all 12 loci should be included to have a significant effect.

Complex regulatory network for rice PH

Previous reports indicated that genes can be pyramided to affect PH. Tomita (2012) showed that pyramiding two semidwarfing genes, *d60* and *sd1*, resulted in a PH that was shorter than that using either *d60* or *sd1*. Hu et al. (2013) reported that a double mutant of *tud1*/*d61* was shorter than either *tud1* or *d61*, although *tud1* and *d61* were already two rice dwarf mutants. Importantly, our present study demonstrated that as much as 12 QTLs can be pyramided to control PH, indicating a complex regulatory network.

Genes controlling PH in rice are involved in the complex regulatory networks of phytohormones, including gibberellins, brassinosteroids, strigolactones, indole-3-acetic acid, abscisic acid, and ethylene (Liu et al. 2018). Other PH regulation pathways with nonhormone factors include cell wall development, cytosolic glutamine synthetic pathway, RNA editing, cell division, ubiquitin-proteasome pathway, and fatty acid metabolism (Liu et al. 2018). It is speculated that the 12 putative loci identified in the present study are involved in multiple regulatory pathways. The markers closest to the 12 loci identified in this study can be used directly in marker-assisted breeding to manipulate PH.

ACKNOWLEDGMENTS

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