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QTL mapping for heading date and plant height using a RIL population in rice in different photoperiod environments

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Abstract: Heading date determines rice seasonal and regional adaptation, while plant height is an important trait related to rice lodging resistance. In this study, a recombinant inbred line population was used to detect quantitative trait loci (QTLs) for both traits in long-day (LD) and short-day (SD) environments. Three and two QTLs for heading date were detected in LD and SD environments, respectively. Notably, *qHD8* and *qHD10* were commonly detected in both environments. Five and four QTLs for plant height were identified in LD and SD environments, respectively. Among them, *qPH3*, *qPH5* and *qPH6* showed no pleiotropic effects on heading date and were detected in both environments. These three QTLs are considered to be the primary targets for improving rice plant height. Additionally, two genomic regions exhibited pleiotropic effects on both heading date and plant height. The alleles delayed the heading date while simultaneously increasing plant height. This study indicated that most QTLs for heading date are sensitive to photoperiod and have pleiotropic effects on plant height, thereby complicating their application in breeding programs. These findings provide useful information for the breeding of rice varieties with desired heading dates and plant heights.

Keywords: gene-environment interaction; genetic mapping; *Oryza sativa* L.; pleiotropic effect; quantitative trait loci

Rice (*Oryza sativa* L.) is one of the most important food crops worldwide. Heading date plays a crucial role in the adaptation of rice to specific seasons and regions (Osnato 2023). Plant height serves as a vital factor impacting lodging resistance, harvest index, and yield potential (Wang et al. 2014). Numerous studies have highlighted the close association between heading date and plant height (Hu et al. 2019). Therefore, comprehending the genetic foundations of heading date and plant height, as well as their

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interrelationship, assumes paramount significance in the pursuit of stable and high-yield rice breeding.

Rice heading date is primarily influenced by factors such as photoperiod, temperature, and nutrient levels, with photoperiod being a significant determinant (Zhou et al. 2021). Rice is a short-day (SD) plant, meaning that heading date is typically promoted under SD conditions but delayed under long-day (LD) conditions. The expression level of florigens plays a crucial role in the regulation of heading date, with higher levels promoting heading and lower levels causing a delay. Consequently, the regulation of rice heading revolves around controlling the expression of florigens. In particular, rice possesses two florigens, *Hd3a* and *RFT1* (Pasriga et al. 2019). In addition, there exist three significant regulatory pathways. The first pathway, known as *OSGI-Hd1-Hd3a*, assumes a crucial role in both LD and SD conditions. The second pathway involves the regulation of *Hd3a* by *Ehd1* specifically under SD conditions. The third pathway entails the regulation of *RFT1* by *Ehd1* exclusively under LD conditions. Notably, the latter two pathways share a common regulator, *Ehd1*. However, it is important to note that under these two conditions, *Ehd1* is subject to distinct upstream regulatory factors that govern its expression (Sun et al. 2022). In summary, the photoperiodic pathway of rice heading date genes can be categorized into three groups, namely, upstream regulators, flowering signal integron genes, and florigens (*Hd3a* and *RFT1*). The majority of heading date genes function as upstream regulators, including *OsMADS51*, *DTH3*, *OSGI*, *Ghd7*, and *Ghd8*. The flowering signals of the upstream regulators are integrated on the flowering signal integron genes *Hd1* and *Ehd1*. Subsequently, the expression of florigens is controlled by the flowering signal integron genes (Zhou et al. 2021).

Several genes that control plant height have been cloned in rice. These genes are associated with the signal transduction and biosynthesis of phytohormones, including gibberellic acid, abscisic acid, and brassinosteroid (Liu et al. 2018). The „green revolution“ gene *Sd1*, which encodes an oxidase enzyme, is involved in the biosynthesis of gibberellin, and deficiency of the *Sd1* gene results in a dwarf phenotype (Sasaki et al. 2002). Additionally, brassinosteroid, a crucial phytohormone, plays a significant role in modulating the plant height of rice. The genes *D2*, *D11*, and *Brd1*, which are involved in the biosynthesis of brassinosteroids, have been found to be correlated with plant height (Castorina & Consonni 2020). Furthermore, it has been reported that genes regulating heading date, such as *Ghd7*, *Ghd7.1*, and *Ghd8*, exhibit pleiotropic effects on heading date, plant height and grain number (Zhou et al. 2021).

Quantitative trait loci (QTLs) pleiotropy is a prevalent phenomenon in rice, particularly in relation to traits such as heading date and plant height. Numerous studies have indicated a correlation between the two traits. Primary mapping studies often detect QTLs for heading date and plant height within the same genomic interval (Han et al. 2017). Additionally, fine mapping and cloning studies have identified several QTLs exhibiting pleiotropy for both traits, many of which are key regulatory genes in the pathway controlling rice heading date (Xue et al. 2008; Yan et al. 2011, 2013; Zhu et al. 2017; Sun et al. 2022; Fan et al. 2023). Consequently, it can be deduced that the pleiotropic effects of heading date QTLs on plant height are a widespread occurrence. Despite the cloning of numerous QTLs for heading date or plant height, whether they are pleiotropic for both traits has not been clearly reported in most studies. In this study, a recombinant inbred line (RIL) population derived from a cross between the restorer lines Qianhui 136 (QH136) and Zhonghui 9308 (ZH9308) was investigated for QTL mapping for heading date and plant height under SD and LD conditions, respectively. Our objectives are to identify QTLs that control heading date and plant height in the RIL population under different photoperiod environments and to determine if these QTLs exhibit pleiotropic effects on both traits. The findings of this study are expected to contribute to a better understanding of the genetic basis of heading date and plant height in rice, as well as the relationship between these two traits, which is of great significance to breeding practice.

MATERIAL AND METHODS

Rice material. QH136 was developed by our team, and ZH9308 was obtained from professor Shihua Chen at the China Rice Research Institute. They are both restorer lines utilized in different regions of China. QH136 is specifically employed in the southwest region, which is known for its relatively high altitude, whereas ZH9308 is utilized in the southeast region, typically characterized by lower altitudes. QH136 was selected as the female parent and crossed with ZH9308. Subsequently, an F_7 RIL population containing 247 lines was developed through the single seed descent method, originating from a single F_2 population.

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Field experiment and trait evaluation. The RIL population and parent materials were grown in Guiyang (GY), Guizhou, China (26°51'N, 106°67'E) during the period of April to September 2019, and in Sanya (SY), Hainan (18°30'N, 109°55'E) from November 2019 to April 2020. The day-length conditions in GY and SY are LD and SD, respectively. The field experiment followed a randomized complete block design with two replications. Within each replication, twelve plants per line were planted in a single row, with a spacing of 16.7 cm between plants and 26.7 cm between rows.

The days from seeding to the heading of the first panicle of an individual were recorded as the heading date (HD). Ten plants located in the middle of each row were selected for measurement of HD. Plant height (PH) was assessed at maturity by measuring the distance between the root neck and the top of the main panicle. Five plants, situated in the middle of the ten plants in each row, were chosen for PH measurement. The average values of each line were used for data analysis.

DNA marker analysis. A total of 460 Indel and 50 SSR markers that were distributed in the whole genome were selected to screen polymorphism between the parents, QH136 and ZH9308 (Table S1 in Electronic Supplementary Material (ESM)). All the Indel markers were designed according to the difference between QH136 and ZH9308 detected by whole-genome resequencing. All SSR markers were selected from the Gramene databases on March 10th, 2021 (http://www.gramene.org/).

The marker assay was carried out as below. During the tillering stage, young leaves of approximately 2 cm were collected from each line. Total DNA was extracted following Zheng et al. (1995). PCR amplification was performed according to Chen et al. (1997), and the products were visualized on 8% non-denaturing polyacrylamide gels using silver staining.

Genetic map construction. A genetic map of the RIL population was constructed using the MAP functionality in QTL IciMapping (Ver. 4.2) (Meng et al. 2015). 143 polymorphic markers, including 137 Indel and 6 SSR markers (Table S1 in ESM), were used for genetic map construction. Genetic distance (centiMorgan, cM) between markers was calculated using the Kosambi function. Linkage groups were determined using a logarithm of the odds (LOD) threshold of 3.0.

Data analysis. QTL analysis was performed using QTL IciMapping (Ver. 4.2) software as described by Meng et al. (2015). ICIM-ADD method was applied for QTL analysis. The LOD thresholds for GY and SY were determined to be 2.80 and 2.82, respectively, through 1 000 permutations with a significance level of $P < 0.05$. QTL nomenclature refers to McCouch and CGSNL (2008).

RESULTS

Phenotypic variation. The performance of HD and PH in the RIL population and parents is given in Table 1. HD and PH of QH136 were higher than those of ZH9308 in GY and SY. Furthermore, the HD and PH values of the RIL population displayed a continuous distribution across both locations (Figure 1).

The HD of the RIL population exhibited a positive correlation with PH in both GY and SY ($P < 0.01$), implying that genes responsible for HD and PH may be located in similar genomic regions or the presence of pleiotropic genes influencing both traits. In addition, the HD and PH of the RIL population in GY were positively correlated with those in SY ($P < 0.01$), which indicates that similar regulators for both traits were constitutively expressed in the two locations.

Linkage map. A linkage map was constructed utilizing evenly dispersed polymorphic markers

Table 1. Phenotypic variation of the recombinant inbred line population and parents

Trait	Location	Mean	SD	Range	Skew	Kurt	*CV*	Parental mean	
								QH136	ZH9308
HD (day)	GY	119.3	6.6	97.1–135.4	–0.6	0.8	5.5	128.8	118.8
	SY	107.7	8.0	84.9–124.5	–0.3	–0.5	7.5	118.2	110.9
PH (cm)	GY	106.8	9.9	73.5–134.9	–0.3	0.4	9.2	108.6	98.4
	SY	100.9	11.2	77.0–128.6	–0.1	–0.5	11.1	115.8	94.6

HD – heading date; PH – plant height; GY – Guiyang; SY – Sanya; SD – standard deviation; Skew – skewness; Kurt – kurtosis; *CV* – coefficient of variation; QH136 – Qianhui 136; ZH9308 – Zhonghui 9308

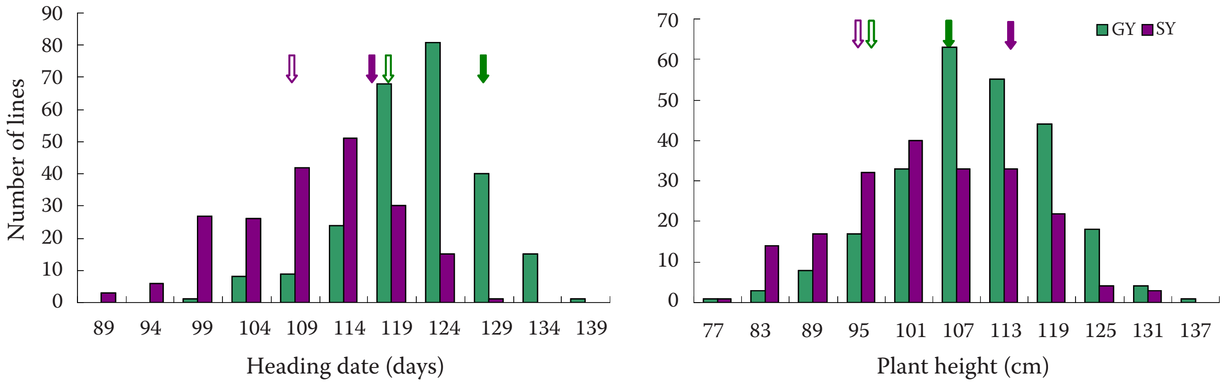

Figure 1. Phenotypic variation in heading date and plant height of the recombinant inbred line population

GY = Guiyang; SY = Sanya; the green and purple arrows indicate phenotypic values of parental lines in Guiyang and Sanya; arrows filled with green and purple colors represent the phenotypic values of Qianhui 136 and Zhonghui 9308

across twelve chromosomes, comprising 137 Indel and 6 SSR markers. The linkage map spanned 1 118.9 cM in length with an average genetic distance of 7.8 cM between adjacent markers. Notably, for chromosome 11, the markers were predominantly concentrated on the short arm due to a lack of polymorphic markers in the remaining region. This may potentially impede the detection of QTLs associated with the target trait.

QTL analysis. For the heading date, a total of three and two main-effect QTLs were detected in GY and SY, respectively (Table 2 and Figure 2). In GY, the QTLs collectively accounted for 42.8% of the observed variation, with a single QTL explaining a range of 10.3% to 20.2% of the phenotypic variation. In SY, the total variation explained by the QTLs was 46.9%, with a single QTL explaining a range of 5.1% to 41.8% of the phenotypic variation. Two QTLs (*qHd8* and *qHd10*) were detected in both locations, while one QTL (*qHd7*) was specifically identified in GY. It was observed that *qHd8* exhibited varying effects across different environments. Specifically, the QH136 allele decreased the heading date by 3.3 days in GY, whereas it led to an increase of 2.1 days in SY. As for *qHd10*, the QH136 allele caused an increase in heading date by 2.5 and 5.8 days, and explained 12.2% and 41.8%

Table 2. Quantitative trait loci (QTLs) for heading date and plant height detected in Guiyang and Sanya

Trait	Location	QTL	Peak (cM)	Left marker	Right marker	LOD	Add	PVE (%)
HD	GY	qHD7	74	I7-27556	I7-28346	10.1	2.3	10.3
		qHD8	12	I8-3656	I8-4361	17.3	–3.3	20.2
		qHD10	57	I10-17516	I10-18444	11.9	–2.5	12.2
	SY	qHD8	22	I8-4361	I8-8340	4.5	2.1	5.1
		qHD10	54	I10-11695	I10-17516	31.0	–5.8	41.8
PH	GY	qPH3	121	I3-31938	I3-35969	7.8	–3.4	8.1
		qPH5	105	I5-23572	I5-24227	4.7	2.6	4.9
		qPH6	83	I6-24348	I6-25218	6.9	3.1	6.9
		qPH7	62	I7-23383	I7-26782	3.0	2.3	3.9
		qPH8	11	I8-3656	I8-4361	6.3	–3.2	7.1
	SY	qPH3	112	I3-31938	I3-35969	3.2	–3.0	5.5
		qPH5	110	I5-24227	I5-27090	4.3	3.0	5.8
		qPH6	83	I6-24348	I6-25218	5.6	3.2	6.4
		qPH10	60	I10-17516	I10-18444	15.5	–5.6	20.3

HD – heading date; PH – plant height; GY – Guiyang; SY – Sanya; LOD – logarithm of the odds; Add – additive effect, the genetic effect when a Zhonghui 9308 allele is replaced by a Qianhui 136 allele; PVE – the proportion of phenotypic variance explained by the given QTL

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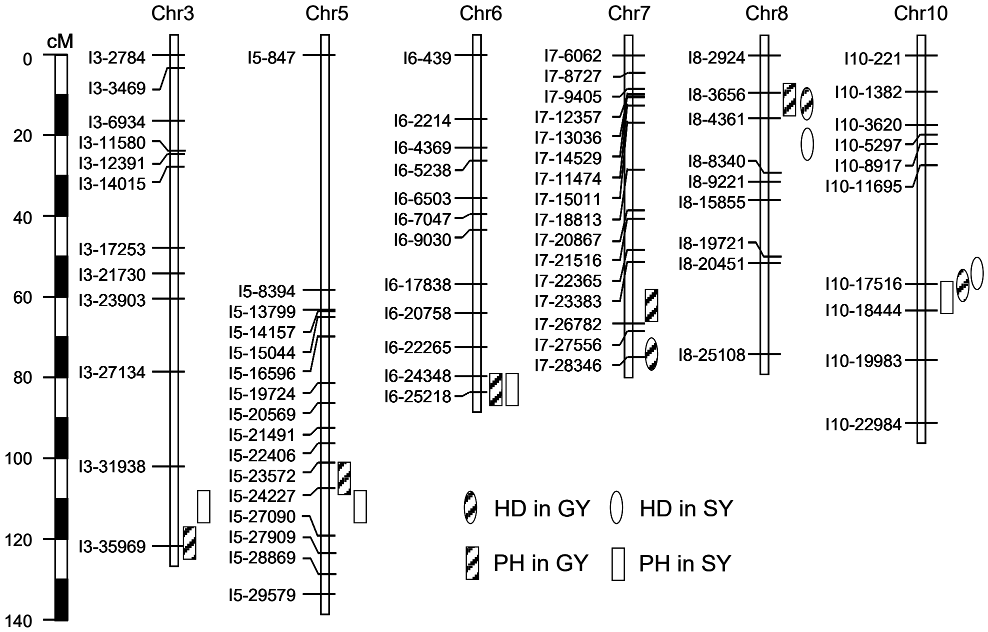

Figure 2. QTLs for heading date and plant height detected in Guiyang and Sanya
HD – heading date; PH – plant height; GY – Guiyang; SY – Sanya

of the phenotypic variation in GY and SY, respectively. Interestingly, although the allele-increasing heading date for qHd10 was consistent from QH136 in both locations, the magnitude of the QTL effect was found to be greater in SY.

For plant height, a total of five QTLs were identified in GY, while four QTLs were detected SY (Table 2 and Figure 2). The five QTLs detected in GY accounted for 31.0% of the phenotypic variation in total, with individual R^2 values ranging from 3.9% to 8.1%. The four QTLs detected in SY jointly explained 38.0% of the phenotypic variation, with R^2 values ranging from 5.5% to 20.3%. Three QTLs (*qPH3*, *qPH5* and *qPH6*) were detected in both locations, while two QTLs (*qPH7* and *qPH8*) were exclusively detected in GY and one QTL (*qPH10*) was exclusively detected in SY.

Two regions showed significant allelic variation for both heading date and plant height (Figure 2). In GY, *qHd8* and *qPH8* were located on the short arm of chromosome 8. The alleles increasing phenotypic values were both from QH136, with *qHd8* exhibiting a more substantial contribution to the phenotypic variation. In SY, *qHd10* and *PH10* were located in the same region on chromosome 10. The alleles increasing phenotypic values were from QH136, with *qHd10* accounting for a greater proportion of the phenotypic variation.

DISCUSSION

Rice heading date and plant height are both important agronomic traits that are governed by quantitative trait loci and susceptible to environmental influences. Photoperiod is a critical factor affecting heading date (Tsuji et al. 2013), while plant height has been found to be closely associated with heading date (Hu et al. 2019). To investigate the genetic basis of heading date and plant height in rice, this study developed an RIL population originating from a cross between the restorer lines QH136 and ZH9308, which are utilized in distinct ecological regions within China. Three and two QTLs for heading date were detected in GY and SY, respectively. Five and four QTLs for plant height were detected in GY and SY, respectively. All QTLs associated with heading date displayed photoperiod sensitivity and exhibited pleiotropic effects on plant height (Table 2). Additionally, three QTLs (*qPH3*, *qPH*5 and *qPH6*) for plant height demonstrated consistent performance across environments making them primary targets for rice breeding.

Rice heading is promoted and inhibited under SD and LD conditions, respectively. This can be attributed to the photosensitivity of heading date QTLs (Hori et al. 2016). The present study identified three major heading date QTLs in two distinct daylength environments, each exhibiting different effects. For *qHD8*, the QH136 allele delayed heading date by 3.3 days under SD condition, with an R^2 of 20.2%, whereas it promoted heading date by 2.1 days under LD condition, with an R^2 of 5.1%. In the case of *qHD10*, despite both delayed heading date alleles were originated from QH136 in the two environments, the QTL effect exhibited significant variation. Specifically, *qHD10* accounted for 41.8% of the phenotypic variance under the LD condition, whereas this value decreased to 12.1% under the SD condition. For *qHD7*, it was solely detected only under LD condition. These QTLs showed sensitivity to photoperiod, with their QTL effects varying across different day-length environments. In addition, they were co-localized with the cloned genes *Ghd7.1*, *Ghd8*, and *Ehd1*, and had consistent response to photoperiod (Doi et al. 2004; Wei et al. 2010; Koo et al. 2013). Therefore, the *qHD7*, *qHD8* and *qHD10* may be allelic to *Ghd7.1*, *Ghd8* and *Ehd1*, respectively. QH136 is a restorer line applied in the upper reaches of the Yangtze River, while ZH9308 is a restorer line applied in the lower Yangtze River. The three detected QTLs for heading date may be important genetic factors accounting for heading date variation of rice cultivars between the two regions. In rice breeding practice, more attention should be given to the photosensitivity of heading date QTLs when it is involved in breeding materials from distinct regions.

Many QTLs have shown pleiotropic effects on both heading date, plant height and grain yield (Hu et al. 2019). For instance, functional alleles of *Ghd7* (Xue et al. 2008), *Ghd7.1* (Yan et al. 2013), *Ghd8* (Yan et al. 2011) and *Hd1* (Zhang et al. 2012) delay heading, increase plant height as well as enhance grain yield under LD conditions. Furthermore, the augmentation in yield potential of rice cultivars is frequently accompanied by an elevation in plant height and growth duration, which will amplify the susceptibility to abiotic stresses and lodging in areas with insufficient light and heat resource, or regions with more typhoons incidence (Roux et al. 2006). In this study, heading date was positively correlated ($P < 0.01$) with plant height in the RIL population. Moreover, the heading date QTLs, *qHD7*, *qHD8* and *qHD10* were co-located with *qPH7*, *qPH8* and *qPH10*, and the positive alleles were from the same parent (Figure 2). Thus, it is important to consider the pleiotropic effects of these QTLs in breeding program. Specifically, in order to make full use of light and heat resources, alleles that delay heading are usually incorporated in a breeding material. However, the pleiotropic effects of these genes on plant height may result in increased plant height, consequently heightening the risk of lodging. To mitigate these negative consequences, breeders could introduce additional alleles that reduce plant height without affecting heading or select heading date QTLs that do not have pleiotropic effects on plant height. Unfortunately, most QTLs associated with heading date in rice, including *Ghd7*, *Ghd7.1*, *Ghd8*, *Hd1*, *RFT1*, and *Ghd2*, have been found to influence plant height through pleiotropy (Xue et al. 2008; Yan et al. 2011, 2013; Zhu et al. 2017; Sun et al. 2022; Fan et al. 2023). While the impact of many heading date QTLs on plant height remains unreported, it is hypothesized that the pleiotropic effect of heading date QTLs on plant height is a widespread occurrence. Fortunately, there are QTLs such as *GNP1* and *qPL5* that control plant height that do not exhibit pleiotropic effect on heading (Wu et al. 2016; Xu et al. 2022). In the present study, three minor QTLs (*qPH3*, *qPH*5 and *qPH6*) for plant height do not exhibit pleiotropic effects on heading date. Furthermore, they had consistent performance in terms of plant height across environments (Table 2). Therefore, these QTLs for plant height should be priority targets in rice breeding.

REFERENCES

Castorina G., Consonni G. (2020): The role of brassinosteroids in controlling plant height in *Poaceae*: A genetic perspective. International Journal of Molecular Sciences, 21: 1191.

Chen X., Temnykh S., Xu Y., Cho Y.G., McCouch S.R. (1997): Development of a microsatellite framework map providing genome-wide coverage in rice. Theoretical and Applied Genetics, 95: 553–567.

Doi K., Izawa T., Fuse T., Yamanouchi U., Kubo T., Shimatani Z., Yano M., Yoshimura A. (2004): *Ehd1*, a B-type response regulator in rice, confers short-day promotion of flowering and controls FT-like gene expression independently of *Hd1*. Genes and Development, 18: 926–936.

Fan X., Wang P., Qi F., Hu Y., Li S., Zhang J., Liang L., Zhang Z., Liu J., Xiong L., Xing Y. (2023): The CCT transcriptional activator Ghd2 constantly delays the heading date by upregulating *CO3* in rice. Journal of Genetics and Genomics, 50: 755–764.

Han Z., Hu W., Tan C., Xing Y. (2017): QTLs for heading date and plant height under multiple environments in rice. Genetica, 145: 67–77.

Hori K., Matsubara K., Yano M. (2016): Genetic control of flowering time in rice: Integration of Mendelian genetics and genomics. Theoretical and Applied Genetics, 129: 2241–2252.

Hu Y., Li S., Xing Y. (2019): Lessons from natural variations: Artificially induced heading date variations for improvement of regional adaptation in rice. Theoretical and Applied Genetics, 132: 383–394.

Koo B.H., Yoo S.C., Park J.W., Kwon C.T., Lee B.D., An G., Zhang Z., Li J., Li Z., Paek N.C. (2013): Natural variation in *OsPRR37* regulates heading date and contributes to rice cultivation at a wide range of latitudes. Molecular Plant, 6: 1877–1888.

Liu F., Wang P., Zhang X., Li X., Yan X., Fu D., Wu G. (2018): The genetic and molecular basis of crop height based on a rice model. Planta, 247: 1–26.

McCouch S.R., CGSNL (Committee on Gene Symbolization, Nomenclature and Linkage, Rice Genetics Cooperative) (2008): Gene nomenclature system for rice. Rice, 1: 72–84.

Meng L., Li H., Zhang L., Wang J. (2015): QTL IciMapping: Integrated software for genetic linkage map construction and quantitative trait locus mapping in biparental populations. Crop Journal, 3: 269–283.

Osnato M. (2023): Evolution of flowering time genes in rice: From the Paleolithic to the Anthropocene. Plant, Cell and Environment, 46: 1046–1059.

Pasriga R., Yoon J., Cho L.H., An G. (2019): Overexpression of *RICE FLOWERING LOCUS T 1* (*RFT1*) induces extremely early flowering in rice. Molecules and Cells, 42: 406–417.

Roux F., Touzet P., Cuguen J., Corre L.V. (2006): How to be early flowering: An evolutionary perspective. Trends in Plant Science, 11: 375–381.

Sasaki A., Ashikari M., Ueguchi-Tanaka M., Itoh H., Nishimura A., Swapan D., Ishiyama K., Saito T., Kobayashi M., Khush G.S., Kitano H., Matsuoka M. (2002): Green revolution: A mutant gibberellin-synthesis gene in rice. Nature, 416: 701–702.

Sun C., He C., Zhong C., Liu S., Liu H., Luo X., Li J., Zhang Y., Guo Y., Yang B., Wang P., Deng X. (2022): Bifunctional regulators of photoperiodic flowering in short day plant rice. Frontiers in Plant Science, 13: 1044790.

Tsuji H., Taoka K., Shimamoto K. (2013): Florigen in rice: Complex gene network for florigen transcription, florigen activation complex, and multiple functions. Current Opinion in Plant Biology, 16: 228–235.

Wang J., Zou D., Zheng H., Zhao H., Liu H., Jiang T. (2014): Genetic relationships between plant height and its components in japonica rice. Agronomy Journal, 106: 1379–1388.

Wei X., Xu J., Guo H., Jiang L., Chen S., Yu C., Zhou Z., Hu P., Zhai H., Wan J. (2010): *DTH8* suppresses flowering in rice, influencing plant height and yield potential simultaneously. Plant Physiology, 153: 1747–1758.

Wu Y., Wang Y., Mi X.F., Shan J.X., Li M.X., Xu J.L., Lin H.X. (2016): The QTL *GNP1* encodes GA20ox1, which increases grain number and yield by increasing cytokinin activity in rice panicle meristems. PLoS Genetics, 12: e1006386.

Xu Z., Li M., Du Y., Li X., Wang RT., Chen Z., Tang S., Liu Q., Zhang H. (2022): Characterization of *qPL5*: A novel quantitative trait locus (QTL) that controls panicle length in rice (*Oryza sativa* L.). Molecular Breeding, 42: 70.

Xue W., Xing Y., Weng X., Zhao Y., Tang W., Wang L., Zhou H., Yu S., Xu C., Li X., Zhang Q. (2008): Natural variation in *Ghd7* is an important regulator of heading date and yield potential in rice. Nature Genetics, 40: 761–767.

Yan W.H., Wang P., Chen H.X., Zhou H.J., Li Q.P., Wang C.R., Ding Z.H., Zhang Y.S., Yu S.B., Xing Y.Z., Zhang Q.F. (2011): A major QTL, *Ghd8*, plays pleiotropic roles in regulating grain productivity, plant height, and heading date in rice. Molecular Plant, 4: 319–330.

Yan W., Liu H., Zhou X., Li Q., Zhang J., Lu L., Liu T., Liu H., Zhang C., Zhang Z., Shen G., Yao W., Chen H., Yu S., Xie W., Xing Y. (2013): Natural variation in *Ghd7.1* plays an important role in grain yield and adaptation in rice. Cell Research, 23: 969–971.

Zhang Z.H., Wang K., Guo L., Zhu Y.J., Fan Y.Y., Cheng S.H., Zhuang J.Y. (2012): Pleiotropism of the photoperiod-insensitive allele of *Hd1* on heading date, plant height and yield traits in rice. PLoS ONE, 7: e52538.

Zheng K.L., Huang N., Bennett J., Khush G.S. (1995): PCR-Based Marker-Assisted Selection in Rice Breeding. IRRI Discussion Paper Series No. 12, Los Banos, International Rice Research Institute.

Zhou S., Zhu S., Cui S., Hou H., Wu H., Hao B., Cai L., Xu Z., Liu L., Jiang L.,Wang H., Wan J. (2021): Transcriptional and post-transcriptional regulation of heading date in rice. New Phytologist, 230: 943–956.

Zhu Y.J., Fan Y.Y., Wang K., Huang D.R., Liu W.Z., Ying J.Z., Zhuang J.Y. (2017): *Rice Flowering Locus T 1* plays an important role in heading date influencing yield traits in rice. Scientific Reports, 7: 4918.

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