Mapping and breeding value evaluation of a semi-dominant semi-dwarf gene in upland rice

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ABSTRACT

Plant height is an important trait related to yield potential and plant architecture. A suitable plant height plays a crucial role in improvement of rice yield and lodging resistance. In this study, we found that the traditional upland landrace ‘Kaowenghan’ (KWH) showed a special semi-dwarf phenotype. To identify the semi-dwarf gene from KWH, we raised BC2F4 semi-dwarf introgression lines (IL) by hybridization of the japonica rice cultivar ‘Dianjingyou1’ (DJY1) and KWH in a DJY1 background. The plant height of the homozygous semi-dwarf IL (IL-87) was significantly reduced compared with that of DJY1. The phenotype of the F1 progeny of the semi-dwarf IL-87 and DJY1 showed that the semi-dwarf phenotype was semi-dominant. QTL mapping indicated that the semi-dwarf phenotype was controlled by a major QTL qDH1 and was localized between the markers RM6696 and RM12047 on chromosome 1. We also developed near-isogenic lines (NIL) from the BC2F4 population, and found that the yield of homozygous NIL (NIL-2) was not significantly different compared to DJY1. Breeding value evaluation through investigation of the plant height of the progeny of NIL (NIL-2) and cultivars from different genetic background indicate that the novel semi-dwarf gene shows potential as a genetic resource for rice breeding.

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Rice (Oryza sativa) is one of the most important cereal crops and is a staple food in many countries worldwide. With the rapid increase in the global population and the emergence of a food crisis, increasing rice yields has become the focus of rice research and breeding programs (Khush, 2005). Plant height is an important rice trait that directly affects the yield and lodging resistance. Dwarf plants show enhanced lodging resistance, but an excessively dwarfed plant leads to inadequate growth and a tendency for densely overlapping leaves, thus reducing rice yield. However, extremely tall plants are susceptible to lodging which also reduces rice yield. Therefore, the discovery and utilization of semi-dwarf genes is of considerable importance for the improvement of rice yield.

In recent years, many genes the modulate plant height, including more than 60 recessive dwarf genes and 10 recessive semi-dwarf genes, have been identified or cloned (Zhang et al., 2014). **DWARF 18 (D18)** is a dwarf gene that encodes OsGA3ox2, which controls rice plant height by participating in gibberellins (GA) biosynthesis (Tong et al., 2014; Iwamoto et al., 2011; Itoh et al., 2001). The dwarf gene gibberellin insensitive dwarf 1 (gid1) encodes a soluble gibberellin receptor that affects plant height by mediating GA signaling transduction in rice (Ayano et al., 2014; Tanaka et al., 2006; Ueguchi-Tanaka et al., 2005). **Brassinosteroid-deficient dwarf 1 (brd1)** encodes a key enzyme involved in rice brassinolide (BR) biosynthesis, and the mutant for which is characterized by a severely dwarfed stem, curved and deformed leaves, crown root, small ear shape and grain size (Mori et al., 2002; Hong et al., 2002). The gene **D61**, which encodes a rice BR receptor kinase involved in BR signaling transduction, reduces plant height (Zhang et al., 2016; Nakamura et al., 2006; Yamamuro et al., 2000). **DWARF**

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KAMIKAWABUNNWI TILLERING (HTD2, also known as D88 or D14), a component of the strigolactones (SLs) signaling pathway, encodes an esterase that is involved in inhibition of branching and negatively regulates the number of tillers (Kagiyama et al., 2013; Liu et al., 2009). WEALTHY FARMER’S PANICLE (WFP, also known as IPA1) encodes a transcription factor that can directly bind to the promoter of the negative regulator FINE CULM 1 (FC1), which controls the growth of tiller lateral buds and thus inhibits tillering. WFP also affects plant height and panicle length by directly regulating the important gene DENSE AND ERECT PANICLE 1 (DEPI), thereby determining the spike type (Zhang et al., 2017a; Lu et al., 2013; Miura et al., 2010).

In contrast to recessive genes, few dominant dwarf genes have been reported. In rice, only a few dominant or semi-dominant dwarf genes, including D53, Sst1, Sdd(t), Ds, TID1, LBD4, Sbr-d, D-h, SBl, Dd7, Sd97, have been reported (Liu et al., 2008, 2018; Zhao et al., 2018b; Piao et al., 2014; Liang et al., 2011; Asano et al., 2009; Miura et al., 2009; Qin et al., 2008; Tong et al., 2007; Wei et al., 2006; Sunohara et al., 2003). However, dominant dwarf genes have special advantages in crop breeding (Qin et al., 2008). For instance, unless both parents carry the same recessive semi-dwarf gene, recessive genes cannot be used in hybrid rice cultivars. Dominant genes can be more easily used when only one parent carries the dominant allele. Thus, the germplasm of the other parent can be widely chosen, sharply reducing time, cost, and labor in breeding work (Qin et al., 2008; Liang et al., 2004). Therefore, it is important to discover and utilize novel dwarf genes, especially dominant genes for breeding dwarf varieties.

The dwarf rice germplasms widely used in commercial production in China include ‘Aijiaonante’, ‘Aizaizhan’, ‘Dee-geo-woo-gen’, which genetic analysis has shown all carry the recessive gene semi-dwarf 1 (sd1) (Chen et al., 2013). The frequent use of limited dwarfism sources may disadvantage the diversification of rice varieties, hinder the genetic improvement process, and cause a bottleneck effect in the genetic background available for developing new rice varieties (Matsuo et al., 1997; Luh, 1980; Hargrove and Cabanilla, 1979). Thus, more useful dwarfism sources are required for rice breeding.

In the present study, we found a unique upland landrace ‘Kao-wenghan’ (KWH) from Yunnan province, which unlike other upland rice landraces shows a semi-dwarf phenotype. Genetic analysis indicated that the semi-dwarf phenotype is semidominant. To identify a potentially novel dominant dwarf gene for rice breeding, we crossed KWH donor male parents with DJY1 to generate homozygous semi-dwarf IL-87 and a mapping population. QTL mapping and breeding value evaluation indicate that we identified a novel semi-dwarf gene which may play an important role in the study of the genetic mechanisms of dominant dwarf and breeding utilization in rice.

1. Materials and methods

1.1. Plant materials

DJY1 is a japonica rice cultivar, and KWH is a unique semi-dwarf landrace of japonica upland rice; both are grown in Yunnan province, China. Progeny of the F1 were obtained by crossing DJY1 with KWH; the F1 individuals were consecutively backcrossed to DJY1 as male and recurrent parent until BC3F1; semi-dwarf IL-87 were developed from the BC3F2 population. The BC3F2 population (2015He483), which comprised 68 plants, were developed for genetic analysis and preliminary QTL mapping by crossing DJY1 (male parent) and the semi-dwarf IL-87 (female parent). The BC3F2 population (2017J187), including 396 individuals developed from the heterozygous BC3F2 plants, were planted for further QTL mapping. To confirm the effect of QTL, we also developed QTL homozygous NIL(NIL-2) from the BC3F1 populations for phenotypic assessment.

For breeding value evaluation, F1 progeny were produced by crossing the NIL-2 with 20 core rice cultivars obtained from the International Rice Research Institute (IRRI). These cultivars are genetically diverse and actively used in international breeding programs on account of their wide range of agronomic attributes, and belong to three genetic background groups: Japonica, Aus and Indica (McNally et al., 2009) (Table S1). The plant height of F1 plants was investigated.

All materials were grown in a paddy field at an experimental station at the Xishuangbanna Tropical Botanical Garden, located in Jinghong, Yunnan Province, China. All F1 and parents were sequentially planted in three rows for each material. DJY1, KWH, IL-87 and NIL-2 were planted in a randomized complete block design with three repeats, each block contained 4 rows with 10 plants per row. All the material was planted within a 27 cm × 15 cm plant space. Agronomic traits were examined for eight randomly selected plants from the center of the block. Field management, including irrigation, fertilization, and pest control followed standard agricultural practices.

1.2. Phenotypic measurements

Plant height (cm) was measured from the ground to the tip of the tallest panicle (awns excluded) at full maturity (Würschum et al., 2015). Panicle length (cm) was measured from the base of the panicle to the tip of panicle (Zhao et al., 2018a). The main tiller of each plant was selected to measure the internode length (cm); n1 was measured from the base of the panicle to the first node below; n2 was measured from the first to the second node, and so on (Wang et al., 2017). All F1, parents, and individuals of mapping populations were measured for plant height; DJY1 and IL-87 were measured for panicle length and internode length. The yield-related traits, including tiller number, effective tiller number, number of primary branches, number of secondary branches, grain number per panicle, setting percentage and 1000-grain weight (g), were all investigated in DJY1 and NIL-2 at the mature stage. Fully filled grains were chosen randomly from each plant for measurement of 1000-grain weight.

1.3. Molecular markers and linkage map

Genomic DNA was extracted from fresh leaves of individual plants and the parents following the method of Edwards et al. (1991). Simple sequence repeat (SSR) markers were selected from the published molecular map of rice (McCouch et al., 2002). The SSR analysis was conducted in accordance with the method of Wu and Tanksley (1993). The genetic linkage map was constructed using QTL IciMapping version 3.2 software (Institute of Crop Science Chinese Academy of Agricultural Sciences, CAAS) with a minimum LOD score of 2.5.

1.4. Data analysis

SPSS version 18 in IBM was used to analyze data. The frequency distribution of plant height in the mapping populations was analyzed. The LSD multiple comparative analysis and the Student’s t-test were used to analyze those data. The threshold of α = 0.05 was considered to be statistically significant, and values of $P < 0.01$ were considered to be highly significant. The QTL controlling plant height was identified by interval mapping analysis using the QTL IciMapping software package.
2. Results

2.1. Phenotypic characteristics of IL-87

To identify phenotypic characteristics of semi-dwarf IL-87, KWH, and DJY1, plant height was measured at the maturity stage (Fig. 1A). There was a significant reduction in plant height of IL-87 (71.97 cm) compared to DJY1 (103.09 cm); specifically, IL-87 plants were 70% of the height of DJY1 plants (Fig. 1A and C). To further determine the changes in plant heights of IL-87, internode length and panicle length of IL-87 and DJY1 plants were measured at maturity. Internode length in IL-87 was significantly shorter than in DJY1 (Fig. 1B and E). In IL-87 plants the average length of each successive internode from the tip to the ground level 18.67, 10.43, 6.24, and 2.05 cm respectively. In contrast, in DJY1 plants, the successive internode lengths were 33.15, 17.65, 11.39, and 4.74 respectively. Average panicle length of IL-87 and DJY1 plants were 18.39 cm and 20.85 cm respectively (Fig. 1B and E). These results revealed that IL-87 has a semi-dwarf phenotype.

2.2. Genetic analysis

DJY1 was crossed with IL-87 to analyze the genetic model of the semi-dwarf phenotype. The plant height of F1 progeny was significantly shorter than that of DJY1 but was taller than IL-87 (Fig. 1D), showing an intermediate plant height. These results indicated that the semi-dwarf trait was a semi-dominant trait. The frequency distribution of plant height of the BC3F2 population (2015H3E483) showed a continuous and trimodal distribution similar to that of the two parents and the intermediate types (Fig. 2A); the BC3F3 population (2017J1E87) also showed a similar distribution (Fig. 2B). These observations suggested that the semi-dwarf trait was controlled by a major QTL.

2.3. QTL mapping of the novel semi-dwarf trait

A total of 452 SSR markers, relatively uniformly distributed throughout the rice genomes, were used to assess polymorphism between IL-87 and DJY1. Fifteen SSR markers were polymorphic

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Fig. 1. Phenotypic characteristics of IL-87 and F1 progeny. (A) Representative whole plant photos of DJY1, KWH, and IL-87 after panicle heading. (B) Comparison of the individual regions of the main stems in DJY1 and IL-87. P, panicle, n, internode. (C) Plant height of DJY1, KWH, and IL-87, as determined by measuring the main tillers. (D) Plant height of DJY1, IL-87, and F1, as determined by measuring the main tillers. (E) Length of the panicle and internodes, as determined using the main stems of DJY1 and IL-87. P panicle, n internode. n = 3, ** indicates extremely significant difference compared with DJY1 (P < 0.01); * indicates significant differences compared with DJY1 (P < 0.05).
and were distributed on chromosomes 1, 4, 10, and 11 in IL-87, which was indicative of genomic introgression from KWH. The genotype of 68 individuals from the BC$_3F_2$ population (2015H3E483) was investigated using the 15 polymorphic SSR markers. QTL analysis showed that a QTL between RM486 and RM12057 was detected, and explained 64.39% of the phenotypic variance in plant height, and the QTL was designated $qDH1$ (Fig. 3A; Table 1; Table S2).

To further localize the target QTL, a larger BC$_3F_3$ population (2017J1E87) containing 396 individuals derived from the original BC$_3F_2$ population (2015H3E483) was constructed by three heterozygous recombinant plants between RM486 and RM12057 on chromosome 1 was detected, and explained 64.39% of the phenotypic variance in plant height, and the QTL was designated $qDH1$ (Fig. 3A; Table 1; Table S2).

To confirm that $qDH1$ was the major QTL controlling the semi-dwarf phenotype, we used the BC$_3F_3$ mapping population to develop a NIL-2 line that was homozygous for $qDH1$ at the chromosomal segment between RM6696 and RM12047. The plant heights of NIL-2 and DJY1 were assessed at maturity. The plant height of NIL-2 was significantly reduced compared with that of DJY1, with no significant difference detected between NIL-2 and IL-87 (Fig. 3C). These results illustrate that $qDH1$ is the major QTL that controlled plant height.

2.4. Yield of DJY1 and NIL-2

To investigate whether the reduction in plant height had a side effect on yield, several yield-related traits were investigated between DJY1 and NIL-2 at the maturity stage. The number of grains per panicle and secondary branches of NIL-2 (57.9 and 6.10 respectively) were significantly reduced compared with those of DJY1 (83.7 and 12.04 respectively). The average 1000-grain weight of the NIL-2 (25.61 g) was also significantly lower than that of DJY1 (30.52 g). However, the number of tillers and effective tillers were significantly increased in the NIL-2 (15.2 and 13.2, respectively) compared with those in DJY1 (9.2 and 8.6, respectively). No significant differences in the number of primary branches and setting percentage were detected. The yield of a single plant of NIL-2 (15.62 g) was less than that of DJY1 (20.13 g), with no statistically significant difference observed (Table 2). These results suggest that the negative effects of $qDH1$ on rice yield are negligible.

2.5. $qDH1$ affects plant height in different types of rice cultivars

To further estimate the effect of $qDH1$ on rice height, NIL-2 was crossed with 20 core cultivars obtained from the IRRI, and 18 F$_1$ progenies were raised (two crosses failed). All F$_1$ progeny were planted under the same conditions in our experimental station and phenotyped for plant height. Among the 18 crosses, the plant height of F$_1$ progeny in nine crosses decreased, whereas the plant height of the F$_1$ progeny in the remaining nine cross groups was unchanged. No significant difference in plant height was observed between the F$_1$ progenies and the parent 'IR64-21’, ‘M 202’, ‘Min-ghui 63’ (MH63), ‘N 22’, ‘Nipponbare’ (Nbp), ‘Sadu-Cho’ (Sadu), ‘Shan-Huang-Zhan-2’ (SHZ2), ‘Zhenshan 97B’ (ZS97B) and ‘Cypress’ (Cyp) (Fig. 4A and C). Plant height of F$_1$ progeny was highly significantly reduced compared with that of the parent ‘Azucena’ (Azu), ‘Dom-Sufid’ (Doms), ‘FR13 A’, ‘Li-Jiang-Xin-Tuan-Hei-Gu’ (LTH), and ‘Pokkali’ (Pok), by about 30%, 20%, 18%, 33%, and 37%, respectively (Fig. 4A and B; Table S3). The F$_1$ progenies of ‘Dular’, ‘Moroberekan’ (Mor), ‘Taiunng 67’ (TNG67), and ‘Aswina’ (Asw) were significantly shorter than the parent by 27%, 10%, 11%, and 21%, respectively (Fig. 4A and B; Table S3). Among them, Azu, Moro, LTH, TNG67 and Doms belonged to the japonica group, ‘FR13 A’ and ‘Dular’ belonged to the Aus group, Asw and Pok were attributed to Indica group (Table S1). These results indicate that homozygous NIL-2 can potentially reduce plant height in different types of rice cultivars from different genetic background.

3. Discussion

Plant height is an important target of crop breeding and is positively correlated with yield within a certain range. A suitable plant height is not only beneficial for the ideal plant type, but also plays an important role in improving the yield potential of rice and the photosynthetic efficiency of the upper leaves (Luo et al., 2012). Since the use of the sd1 gene in the ‘Green Revolution’ of rice, an increasing number of plant height genes have been identified and cloned. However, many of them cannot be used for breeding due to unwanted phenotypes such as extreme dwarfsim, sterility, and short grain (Sakamoto et al., 2004). Dominant dwarf genes are of great value and widely used in crop breeding (Liang et al., 2011). The ‘Green Revolution’ genes of wheat, Rht1 and Rht2, are dominant dwarf genes, have been successfully used in wheat breeding (Kurkiev et al., 2007; Gale et al., 1985). In this study, we used the...
japonica cultivar DJY1 and a KWH donor to develop the near-isogenic line NIL-2, which has the semi-dominant dwarf QTL \( qDH1 \). The semi-dominant semi-dwarf QTL \( qDH1 \) was localized between the markers RM6696 and RM12047 on chromosome 1 and we found that \( qDH1 \) reduces rice plant height with few side effects on yield.

In recent decades, a large number of plant height QTLs have been detected in the rice genome. Bao et al. (2009) used

![Diagram](image)

**Fig. 3.** Mapping of QTL for the semi-dwarf trait. (A) The results of QTL mapping based on the BC\(_{3}\)F\(_2\) population (2015H3E483). (B) The results of QTL mapping based on the BC\(_{3}\)F\(_3\) population (2017J1E87). (C) Plant height of DJY1, NIL-2, and IL-87, as determined by measuring the main tillers. \( n = 3 \), ** indicates extremely significant difference compared with DJY1 (\( P < 0.01 \)).

### Table 1
QTLs detected for plant height in the population after two generations.

| Populations name | QTL | Flanking marker | Trait | LOD  | Variance explained (%) | Additive effect |
|------------------|-----|-----------------|-------|------|------------------------|----------------|
| 2015H3E483       | \( qDH1 \) | RM486-RM12057   | height| 11.9117 | 64.3906                | 10.4982         |
| 2017J1E87        | \( qDH1 \) | RM6696-RM12049  | height| 34.1495 | 35.7837                | 6.3784          |

### Table 2
Yield of DJY1 and NIL-2.

| Traits                        | DJY1     | NIL-2     | P-value |
|-------------------------------|----------|-----------|---------|
| Number of gain per panicle    | 83.70 ± 19.06 | 57.90 ± 9.11* | 0.0211  |
| Setting percentage            | 79.44% ± 8.91% | 81.01% ± 8.29% | 0.7788  |
| Number of tillers             | 9.20 ± 1.48  | 15.20 ± 4.66* | 0.0252  |
| Number of effective tillers   | 8.60 ± 1.67  | 13.20 ± 2.58* | 0.0102  |
| 1000-grain weight (g)         | 30.52 ± 1.72 | 25.61 ± 0.46** | 0.0001  |
| Number of primary branches    | 8.57 ± 1.22  | 7.43 ± 0.54  | 0.0858  |
| Number of secondary branches  | 12.04 ± 4.02 | 6.10 ± 1.97** | 0.0141  |
| Theoretical yield of single plant (g) | 20.13 ± 3.49 | 15.62 ± 3.33 | 0.0701  |

\( N = 3 \), **\( P < 0.01 \) by Student’s t-test; *\( P < 0.05 \) by Student’s t-test.
qDH1 induces reduction of plant height in DJY1, but has no negative effects on yield (Fig. 1B; Table 2). Hybridization of NIL-2 with 20 core rice cultivars belonging to three genetic background groups (Table S1), and assessment of the plant height of the F1 progeny showed that qDH1 could reduce the plant height of nine cultivars from different genetic background. Because plant height is a phenotype controlled by multiple genes (Ni et al., 2009; Jaiswal et al., 2002), the interactions between these genes determine plant height differences (Wade, 2001). This may explain why plant height was affected in only half the cultivars examined.

The well-characterized semi-dwarf gene sd1 was also located between the markers RM6696 and RM12047 on chromosome 1. sd1 is a recessive gene located on the long arm of chromosome 1 and reduces rice plant height with few side effects on yield (Hedden, 2003). The QTL qDH1 also presents a similar phenotype. Thus, we speculate that qDH1 might be the dominant allele of sd1. However, in our study, the QTL qDH1 was semi-dominant. If QTL qDH1 is an allele of sd1, it will be important for studying the molecular mechanisms by which different alleles change from recessive to dominant.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.pld.2018.09.001.

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