Inheritance and identification of molecular markers associated with a novel dwarfing gene in barley

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Abstract

Background: Dwarfing genes have widely been used in barley breeding program. More than 30 types of dwarfs or semidwarfs have been reported, but a few has been exploited in barley breeding because pleiotropic effects of dwarfing genes cause some undesired traits. The plant architecture of newly discovered dwarfing germplasm “Huai11” consisted of desirable agronomic traits such as shortened stature and early maturity. Genetic factor controlling the plant height in dwarf line Huai11 was investigated.

Results: The Huai11 was crossed with tall varieties Monker, Mpyt, Zhenongda 3, Zaoshu 3, Advance, Huadamai 1, Huadamai 6, Hyproly and Ris01508. All the F2 plants displayed tall trait. Both tall and dwarf plants appeared in all the F2 populations with a 3:1 segregation ratio, suggesting that dwarfism of Huai11 is controlled by a single recessive gene, btwd1. Allelism test indicated that this dwarfing gene in the Huai11 is nonallelic with the gene br, uz, sdw1 and denso. Using a double haploid population derived from a cross of Huadamai 6 and Huai11 and SSR markers the novel dwarfing gene was mapped onto the long arm of chromosome 7H, and closely linked to Bmac031 and Bmac167 with genetic distance of 2.2 cM.

Conclusion: Huai11 is a new source of dwarf for broadening the genetic base of dwarfism. This dwarf source was controlled by a recessive dwarfing gene btwd1, was mapped onto the long arm of chromosome 7H.

Background

Dwarfism is a valuable trait in crop breeding, because it increases lodging resistance and decreases damages due to wind and rain [1]. Successful use of a dwarfing gene is critical for developing dwarf cultivars [2]. In barley, more than 30 types of dwarfs or semidwarfs have been found including ‘brevariatatum-ari’, ‘brachytic-br’, ‘curly dwarf-cud’, ‘denso dwarf-denso’, ‘erectoides-ert’, ‘lazy dwarf-lzd’, ‘many noded dwarf-mnd’, ‘narrow leaf dwarf-nld’, ‘semi-dwarf-sdw’, ‘single node dwarf-sid’, ‘slender dwarf-sld’, ‘uzu or semibrachytic-uzu’ and ‘vegetative dwarf-dwf’ [2-5]. However, only a few of them have successfully been used in barley breeding program. The dwarfing gene uzu on the chromosome 3HL has widely been used in barley breeding in China, Japan and Korea peninsula [6-10]. The dwarfing gene sdw1 (named as sdw previously) and denso have been used in feed barley breeding in North America and Australia [11-13], and in barley breeding in European [2,13], respectively. The sdw1 and denso genes are allelic [14-17], and were mapped onto the same region of chromosome 3HL and tagged with a RFLP marker MWG 847 by 0.6 cM [12,18,19].

Some of the dwarfing genes have rarely or never been used in barley breeding programs, although have been genetically characterized. For example, the dwarfing gene Gpert or ari-e was mapped on chromosome 5H [5,20,21]. The recessive GA3-insensitive dwarfing genes Rht-H1 and Dwf2 were mapped on the centromeric region of chromosome 2H [22], and on the short arm of 4H [16,23], respectively. Two recessive dwarfing mutants, gai and gal were mapped on the centromere region and on the long arm of 2H, respectively [24]. In 1993, we found a dwarf individual in field of barley landrace ‘Daofu Bai Qing Ke’ in Daofu County, Sichuan. Plant height of ‘Daofu Bai Qing Ke’ is about 119 cm, while height of the dwarf individual is only about 40 cm. The dwarf individual is naked six-rowed barley, and its maturation date is about 4 days earlier than ‘Daofu Bai Qing Ke’. Multi-year and -location experiments showed that the dwarfism is stable. The dwarf line was named as ‘Huai11’.

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Genetic factor controlling plant height of the barley dwarf line Huaai 11 was investigated in the present study. Here we reported the results of genetic analysis and molecular mapping of this novel dwarfism gene.

Methods

Plant materials and field experiments

Plant height of Huaai 11 and other four agronomic traits were evaluated for seven years at two locations (Yaan, Sichuan Province, and Wuhan, Hubei Province). The results showed that dwarfism is constantly expressed with height of 40.8 ± 1.84 cm (Table 1). Its maturity is about 7 days earlier than the control Zaoshu 3 (early maturity variety).

For genetic analysis, Huaai 11 was crossed with tall varieties Monker, Mpyt, Zhenongda 3, Zaoshu 3, and Advance. The 5 F2 populations, their F1 and parents were planted in field in 1998. Additional 4 tall varieties, Huadamai 1, Huadamai 6, Hyproly and Ris01508 were crossed with Huaai 11 in year 2000. The 9 F2 populations, their F1 and parents were planted in 2002 (Table 2).

To test the allelic relationship of Huaai 11 with other dwarfing genes in barley, The F1 of Huaai 11 × Monker that is a popular commercial cultivar developed in USA was crossed with four dwarf varieties, Himalaya (br, 65.7 cm), Aiganqi (uzu, 71.7 cm), India dwarf (sdw1, 61.3 cm) and Maris Mink (denso, 69.2 cm).

All abovementioned generations and their parents were grown on the Experimental Farm of Huazhong Agricultural University, Wuhan. A randomized complete block design with three replications was adopted. The materials were planted in five-row plots with a row length of 1.1 m.

To map the dwarfism gene in Huaai 11, a population consisting of 122 doubled-haploid (DH) lines was developed from a cross between a common feed barley cultivar Huadamai 6 and Huaai 11 using anther culture in this study. The DH population and parents were planted on the Experimental Farm of Huazhong Agricultural University, Wuhan, China. The field trials were conducted following a randomized complete block design with three replications in 2006, 2007 and 2008, respectively. Each of the DH and parental lines were grown in three rows in a plot of 0.6 × 1.5 m².

Height of plants before ripening was measured in the field from soil surface to top of the main culm (with the spike). The height was calculated as the mean of the twelve plants (in three replicates, four plants from each replicate were measured).

Extraction of genomic DNA

The leaves from each doubled-haploid (DH) lines and parents were collected and frozen for DNA extraction. The cetyltrimethylammonium bromide (CTAB) method was used to extract genomic DNA from about 0.6-1.0 g of young leaf-tissue of each accession [25]. The quality of DNA was checked using 0.8% agrose gel electrophoresis, and the DNA concentration was measured using spectrophotometer. Twelve extremely tall lines and twelve short lines were selected from the DH population to construct two DNA pools.

SSR genotyping and mapping analysis

Three-hundred and six SSR markers distributed on all seven barley chromosomes were used to screen polymorphism between the two parental lines. The polymorphic SSR markers were further used to analyze the

| Year     | Location | Height (cm) | Days from Seedling emerging to heading | No. of Spikelets | No. of spikes per plant | Weight per1000 grains |
|----------|----------|-------------|----------------------------------------|------------------|------------------------|-----------------------|
| 1993-1994| Yaan     | 39.9        | 138                                    | 56               | 4.8                    | 26.5                  |
| 1994-1995| Wuhan    | 41.4        | 141                                    | 54               | 5.1                    | 25.7                  |
| 1996-1997| Wuhan    | 41.8        | 142                                    | 61               | 5.5                    | 23.6                  |
| 1997-1998| Wuhan    | 43.2        | 140                                    | 56               | 6.1                    | 24.7                  |
| 2007-2008| Wuhan    | 37.8        | 132                                    | 48               | 5.0                    | 24.1                  |
| 2008-2009| Wuhan    | 39.5        | 127                                    | 54               | 8.6                    | 24.9                  |
| 2009-2010| Wuhan    | 42.1        | 138                                    | 63               | 10.8                   | 25.4                  |
| Mean     |          | 40.8        | 136.9                                  | 56               | 6.6                    | 25.0                  |
| SD       |          | 1.84        | 5.43                                   | 4.933            | 2.28                   | 0.98                  |
two DNA pools. The polymorphic markers between the two bulks were used to genotype the 122 individuals from the DH population. Genotyping data of 122 DH lines were given in Additional file 1 (Table S1).

Polymerase chain reaction (PCR) was carried out in a final volume of 15 μL, containing 3 μL of genomic DNA, 1.5 μL of 10× PCR buffer (with 15 mM Mg2+), 0.3 μL of 10mM NTP mixture, 2.0 μL of a 2.5 μM solution of the forward and reverse primers, and 0.6 units of Taq DNA polymerase (TakaRa Biotechnology, Dalian, China). DNA amplifications were performed in a thermocycler using the following touchdown PCR protocol: 1 cycle of 3 min at 94°C, followed by 15 cycles 94°C for 30 sec, 30 sec at 60°C (decreasing 1°C per cycle), 45 sec at 72°C. Another 25 cycles of 30 sec at 94°C, 30 sec at 50°C, 45 sec at 72°C. The reaction ended with a 5 min extension at 72°C. PCR product was separated on separated on 6% denaturing polyacrylamide gel and visualized using silver staining.

Linkage map was constructed using the software MAPMAKER [26] and the genetic distance (centimorgan, cM) was derived using Kosambi function [27].

Results

Inheritance of the dwarf gene in Huaai 11
Huaai 11 was discovered from the barley landrace Daofu Bai Qing Ke in 1993. Plant height of Huaai 11 is about 40 cm which is significant shorter than Huadamai 6 (85 cm) (Figure 1). Huaai 11 was crossed with nine tall varieties, Monker, Mpyt, Zhenongda 3, Zaoshu 3, Advance, Huadamai 1, Huadamai 6, Hyproly and Ris01508. All the F1 plants were tall. Distribution of plant height in all F2 populations are discontinuous, the distribution curves are dropped to valley at 60 cm, the plant equal or higher than 60 cm was classified as tall, while less than 60 cm as dwarf. Both the tall and dwarf plants appeared in all the F2 populations with a 3:1 segregation ratio for tall : dwarf (plant height ≥ 60 cm : plant height < 60 cm), suggesting that the dwarf trait in the Huaai 11 is controlled by single recessive gene. This gene is designated as btwd1.

The DH population was constructed from the crosses between Huadamai 6 and Huaai 11 varieties. The averages of plant height of Huadamai 6 and Huaai 11 were 82.8 cm and 39.8 cm in three years, respectively. Figure 2 shows the distribution of plant height in the DH population in year 2007-2008. Plant height of the DH lines showed a bimodal distribution, ranging from 25 to 80 cm (Figure 2). The segregation ratio between tall and dwarf is 1:1.

Allelic relationship between btwd1 and other dwarfing genes in barley
Plant height of Huaai 11 (40 cm) is much shorter than that of several other dwarf varieties such as Himalaya (br, 65.7 cm), Aiganqi (uzu, 71.7 cm), India dwarf (sdw1, 61.3 cm) and Maris Mink (denso, 69.2 cm). To test whether Huaai 11 shares the same allele with those four dwarf varieties, the F1 of Huaai 11 × Monker was crossed with those four varieties. All progeny in the four crosses are tall (Table 3), suggesting that the gene btwd1 controlling plant height in the Huaai 11 is nonallelic with the genes in these four dwarf varieties.

Molecular mapping of the dwarf gene btwd1 in Huaai 11
Out of the 306 SSR primers screened, ninety-six are polymorphic between parental lines Huadamai 6 and Huaai 11. The polymorphic SSR markers were used to
confirmed using the individuals that were used to construct the two DNA pools, suggesting that the gene \( btwd1 \) controlling plant height of Huai 11 was located on chromosome 7H. The four polymorphic markers were used to analyze the 122 individuals of DH population. Linkage analysis between SSR markers and plant height found that the dwarfing gene was located on the long arm of chromosome 7H, associated with the marker Bmac167 and Bmac031 at a genetic distance of 2.2 cM (Figure 3).

### Discussion

Utilization of dwarfing genes in barley breeding programs has greatly increased barley yields, particularly in Asia and Europe [28]. In barley, more than 30 types of dwarfs or semidwarfs have been reported. However, because pleiotropic effects of dwarf genes cause some other undesired agronomic traits such as reduced weight and yield [29,30], a few have been exploited in barley breeding. The plant architecture of newly discovered dwarf germplasm Huai 11 consisted of desirable agronomic traits such as shortened stature and early maturity. It is a new source of dwarfs for broadening the genetic base of dwarfism. The segregation ratio (3:1) of tall : dwarf in the all crosses in two years suggested that dwarfism in Huai 11 is controlled by a single recessive gene, \( btwd1 \).

The allelism test of Huai 11 with four dwarf varieties, Himalaya (\( br \)), Aiganqi (\( uzu \)), India dwarf (\( sdw1 \)) and Maris Mink (\( denso \)) showed that all progeny derived from test crosses between the \( F_1 \) of Huai 11 × Monker and those four varieties are tall (Table 3). Since the dwarfism of Huai 11 is controlled by a Mendelian recessive allele, the \( F_1 \) of Huai 11 × Monker was tall as the tall parent. If the Huai 11 is allelic with one of the four dwarf varieties tested here, the progeny will be expected
to have tall : dwarf ratio of 1:1. No dwarf plants from the four crosses were observed, suggesting that the gene \textit{btwd1} controlling plant height in the Huaai 11 is nonallelic with the gene \textit{br}, \textit{uzu}, \textit{sdw1} and \textit{denso}.

In barley, most of the dwarf and semi-dwarf genes were mapped on the chromosome 2H, 3H and 4H. Tsuchiya reported that two loci, the \textit{br1} locus on the short arm of chromosome 7 (7H) and \textit{br2} on the short arm of chromosome 4 (4H) [31,32]. Recently, Yu et al. mapped a semi-dwarfing QTL PH-7 on chromosome 7HL [28]. In our study, the dwarfing gene \textit{btwd1} was mapped on the long arm of chromosome 7H. The chromosome location of \textit{btwd1} is different from the \textit{uzu} (3HL) [9,33,34], \textit{sdw1/denso} (3HL) [18,19], which further demonstrated that the \textit{btwd1} in Huaai 11 is nonallelic with \textit{br2}, \textit{uzu sdw1/denso} genes. The \textit{br1} was mapped on 7HS, while the \textit{btwd1} was mapped on 7HL, indicating that they belong to different locus, and are non-allelic.

The QTL PH-7 was located between the markers BpPb4541 and BpPb3107 on chromosome 7HL [28]. Examining the 7H linkage maps of Varshney et al. [35] and Yu et al. [28] revealed that QTL PH-7 is close to the distal of the 7HL, far away from centromere, while the \textit{btwd1} in Huaai 11 is linked with Bmac167 that is close to the centromere of 7H, suggesting that the \textit{btwd1} in Huaai 11 is different from QTL PH-7.

Most barley cultivars developed in China are dwarfs and semi-dwarfs since 1950 [2]. The study on origin of

| Cross                  | Generation | No. of total plants | No. of dwarf plants (< 60 cm) | No. of high plants (≥60 cm) | \( \chi^2 \) (1:1) |
|------------------------|------------|---------------------|------------------------------|-----------------------------|------------------|
| Huaai11/Monker/Huaai 11| BC1        | 135                 | 62                           | 73                          | 0.90             |
| (Huaai11/Monker)/Aiganqi| TC1        | 119                 | 0                            | 119                         | 0                |
| (Huaai 11/Monker)/Himalaya| TC1    | 157                 | 0                            | 157                         | 0                |
| (Huaai 11/Monker)/Indian dwarf| TC1   | 117                 | 0                            | 117                         | 0                |
| (Huaai 11/Monker)/Maris Mink | TC1    | 143                 | 0                            | 143                         | 0                |

\( \chi^2 \), oen = 3.841.
dwarfing genes used in barley breeding in China indicated that 68.4% of dwarf and semi-dwarf barley cultivars were derivatives of Chibadaimai, Xiaoshanlixiahuang, Cangzhoulouodai, Aiganqi, Zhepi 1 and Yanfu Aizao 3 [2]. Allelism test indicated that Chibadaimai, Xiaoshanlixiahuang, Cangzhoulouodai, and Aiganqi carried the same dwarfing gene uzu on 3HL [9,33,34]. Zhepi 1 and Yanfu Aizao 3 likely are mutations at the sdw1 locus [2]. The dwarfing gene btwd1 in Huaiai 11 is non-allelic with the uzu and sdw1 which have widely been used in China, and provides barley breeders with a new gene in China. Quite often, when breeders use the dwarfing gene to reduce plant height, due to the confounded effects of other loci controlling plant height and environmental effects, not all plant carrying the dwarfing gene can be easily identified [28]. Thus, the linked SSR markers identified in the present study can provide a useful marker-assisted selection tool to transfer the dwarfing gene btwd1 into elite barley germplasm.

Conclusions
Our study indicated that the dwarfing gene btwd1 in Huaiai 11 is non-allelic with the uzu and sdw1 which have widely been used in China, and provides barley breeders with a new gene in China. Linkage analysis located the gene btwd1 gene (btwd1) onto the long arm of chromosome 7H, and it is closely linked to Bmac031 and Bmac167 with genetic distance of 2.2 cM.

Additional material

Additional file 1: Table S1 Genotyping data of 122 DH lines (*A: Plant height < 60 cm, B: Plant height ≥ 60 cm in btwd1).

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Authors’ contributions
XFR is the major executive person in this study, including phenotyping of plant height, marker genotyping and statistical analysis. WWG assisted in phenotyping and marker genotyping. DFS and GLS conceived the design of this study, coordinated the experiments, and wrote the manuscript. CDL produced the Huadama 6 and Huai 11 DH population using the anther-culture method. All authors have read and approved the final manuscript.

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