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ORIGINAL ARTICLE

Identification of a *Sidwf1* gene controlling short internode length trait in the sesame dwarf mutant *dw607*

Hongmei Miao[1] · Chun Li[1] · Yinghui Duan[1] · Libin Wei[1] · Ming Ju[1] · Haiyang Zhang[1]

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Abstract

Key message ***SiDWF1*** **encodes a gibberellin receptor GID1B-like protein controlling the internode length and plant height in sesame.**

Abstract Sesame is a high-height crop. Here we systematically analyzed the morphological and genetic characters of the sesame dwarf mutant *dw607* (*dwf1* type). The plant height and the internode length of *dw607* significantly declined, while the thousand seed weight (TSW) significantly increased ($P < 0.01$). The cell size of stem parenchyma and pith tissue reduced, and vascular bundle cells and parenchyma tissue arranged much tighter in the dwarf mutant. Based on the cross-population association mapping of a RIL population of the cross '*dw607* (*dwf1*) × 15N41 (wt type),' the target interval linked to the short internode length was located on C9.scaffold2 of SiChr.4 in sesame. We further screened the 58 variants using the genomic variant data of 824 germplasm and BSA DNA pools and determined the target gene *Sidwf1*. The SNP mutation of C_{1057} to T_{1057} resulted in the amino acid change of P_{150} (proline) to S_{150} (serine) in SiDWF1. *SiDWF1* gene allele is 1,638 bp and encodes a gibberellin receptor GID1B-like protein. Transcription profile assay reflected that *Sidwf1* is highly expressed in leaf, stem, bud, and capsule tissues. The dynamic variation in endogenous GA_3 content in *dw607* and the wild type was also monitored in this study. The results revealed the molecular genetic mechanism of the internode length and plant height trait in sesame for the first time. The findings supply the theoretical and material basis for developing the marker-assisted selection (MAS) breeding in sesame.

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✉ Haiyang Zhang
zhanghaiyang@zzu.edu.cn

Hongmei Miao
miaohongmeichina@yahoo.com

Chun Li
agronome@163.com

Yinghui Duan
duanyly@aliyun.com

Libin Wei
libinwei2013@aliyun.com

Ming Ju
jumingzz@163.com

[1] Henan Sesame Research Center, Henan Academy of Agricultural Sciences, Zhengzhou 450002, Henan, People's Republic of China

Abbreviations

ABA	Abscisic acid
BR	Brassinosteroid
BSA	Bulked segregant analysis
DAS	Days after sowing
ELISA	Enzyme-linked immunosorbent assay
EMS	Ethyl methanesulfonate
Ep	Epidermis
FAA	Formalin–glacial acetic acid–alcohol
GAs	Gibberellins
GID1	Gibberellin-insensitive dwarf 1
GLM	General linear model
GWAS	Genome-wide association studies
IAA	Indole-3-acetic acid
InDel	Insertion–deletion
LG	Linkage group
JA	Jasmonate
KEGG	Kyoto Encyclopedia of Genes and Genomes
MAS	Marker-assisted selection
NGS	Next-generation sequencing technology
NR	Non-redundant
PC	Parenchyma cell

PE	Paired end
Pi	Pith
qRT-PCR	Quantitative real-time PCR
QTL	Quantitative trait loci
RIL	Recombinant inbred line
SNP	Single-nucleotide polymorphism
TSW	Thousand seed weight
VC	Vascular bundle cells

Introduction

Sesame (*Sesamum indicum* L., $2n = 26$) is an important and specific oilseed crop with high nutrition and oil quality (Zhang et al. 2019). Sesame seeds contain abundant nutritional substances including oil (50–55%), proteins (18–20%), carbohydrate (13–25%), digestible fiber (high to 9.8%), and antioxidants (high to 1.1%) (Jimoh and Aroyehun 2011; Zhang et al. 2012, 2019; Makinde and Akinoso 2013; Prakash and Naik 2014; Sene et al. 2017). At present, sesame is cultivated mainly in the developing countries for its labor-consuming production process. Sesame is a high-height crop with long stem or branches. Plant height is positively correlated with seed yield. However, sesame varieties with higher height and longer capsule stems are more susceptible to lodging damage by strong wind or hurricanes and bring about more difficulties for mechanized harvest (Langham et al. 2002; Langham 2008; Zhang et al. 2019). Thus, reducing plant height as well as increasing or stabilizing the final seed yield is one of the crucial breeding objectives in sesame.

Plant height is one of the most important agronomic traits for crops (Li et al. 2018a). Dwarfing and semidwarfing mutations can affect the plant height and contribute to high lodging resistance and yield, as the maturity and harvest index of dwarf and semidwarf mutants are always stimulated (Ashikari et al. 1999). As dwarf wheat lines have been applied since the 1960s, the world wheat production significantly increases. Till now, hundreds of dwarf and semidwarf mutants with short internode length have been found for many crops. Dozens of genes regulating the dwarf and semidwarf phenotypes have been cloned from wheat, maize, rice, soybean, and other plants (Peng et al. 1999; Sasaki et al. 2002; Feng et al. 2015; Thomas 2017; Wang et al. 2017b; Li et al. 2018a, b). Moreover, a great deal of studies revealed that the dwarf or semidwarf phenotype in most mutants was associated with the content variation in endogenous hormones, such as gibberellins (GAs), indole-3-acetic acid (IAA), auxin, brassinosteroid (BR), and Jasmonate (JA) (Rebetzke et al. 2011; Feng et al. 2015; Kurotani et al. 2015; Avila et al. 2016; Hirano et al. 2017; Wang et al. 2017b). In wheat, the reduced height 1 (Rht-1) dwarfing mutation was regulated by either of *Rht-B1b* and *Rht-D1b* (also named 'green evolution genes') (Peng et al. 1999; Thomas 2017). The results proved that *Rht-B1b* and *Rht-D1b* encode the short N-terminal GID1-GA binding peptide fragments which are required for binding the GID1-GA receptor complex and promoting GA-responsive growth. Nucleotide substitution and premature stop codon formation of *Rht-B1b* and *Rht-D1b* resulted in the truncated products and the dwarfism in wheat. Similarly, a gene *sd-1* identified from a semidwarf rice mutant Dee-Geo-Woo-Gen-type *sd-1* was proved to encode a gibberellin 20 oxidase and took part in the gibberellin biosynthesis pathway (Monna et al. 2002). A 383-bp deletion from exon 1 to exon 2 resulted in a frameshift and the formation of a termination codon and finally affected the gene expression (Monna et al. 2002).

For sesame, previous studies indicate that plant height trait is a quantitative trait (Sharmila et al. 2007; Satish 2013). Dozens of QTLs and SNP markers linked with plant height were identified in sesame (Wei et al. 2015; Wang et al. 2016). However, to our knowledge, no genes controlling the plant height trait have been cloned in sesame till now. Recently, a dwarf mutant *dw607* (*dwf1* type) has been created using ethyl methanesulfonate (EMS) mutagenesis by Chinese sesame scientists (Wang et al. 2017a). Compared with the wild type (Yuzhi 11), the plant height of *dw607* declined by more than 40%, and the internode length reduced about 50%. More importantly, the yield of dwarf varieties derived from *dw607* significantly increased under rich fertilizers and water culture conditions (data not shown). Thus, creation of dwarf mutant *dw607* supplies a valuable material for exploring the genetic mechanism of plant height trait and dwarf variety breeding in sesame.

Here, the objectives of this study are: (1) to systematically investigate the morphological characteristics of the sesame dwarf mutant *dw607*; (2) to identify the first sesame dwarf gene *Sidwf1* using a RIL population derived from mutant *dw607* and wild type with normal internode length and plant height traits using the high efficient mapping association and genome-wide variants screening method; and (3) to exploit the mutagenesis character and expression profiles of *SiDWF1* gene alleles in sesame. The findings supply the theoretical basis for developing the molecular marker-assisted selection (MAS) breeding in sesame.

Materials and methods

Plant materials and populations

A dwarf mutant *dw607* with the short internode length was induced from a subline (90-1) of Yuzhi 11 using EMS mutagenesis (Zhang et al. 2019). The mutant *dw607* and the wild type (var. Yuzhi 11) as control were cultured at the Yuanyang Experimental Station (113°97′E and 35°05′N) for

phenotype trait investigation and histological and physiological analysis during 2013–2016. Two cross-combinations of *dw607* (*dwf1*, P_1) × Yuzhi 11 (wt, P_2) and *dw607* (*dwf1*, P_1) × 15N41 (wt, P_2) and the six generation populations (i.e., two parents, F_1, BC_1, BC_2, and F_2) of each combination were cultured for target trait segregation analysis in 2012 and 2013 (Table 2).

The 113 F_6 individuals of the RIL population derived from *dw607* and 15N41 and the two parents were cultured at Sanya Experimental Station (109°50′E and 18°25′N) for genome re-sequencing and target gene location in 2013. Other 100 individuals with *dwf1* and wt genotype, respectively, were chosen from the $F_{2\text{-}3}$ population of *dw607* (*dwf1*, P_1) × Yuzhi 11 (wt, P_2) and applied to construct two DNA BSA (bulked segregant analysis) pools for Illumina sequencing. A total of 600 $F_{2\text{-}3}$ lines of the combination population of *dw607* (*dwf1*, P_1) × Yuzhi 11 (wt, P_2) were collected at Yuanyang Experimental Station for candidate SNP validation in 2014. Meanwhile, 500 germplasm accessions (partial list in Supplementary Fig. 2) with normal internode length trait were randomly chosen from the sesame germplasm reservoir of Henan Sesame Research Center, Henan Academy of Agricultural Sciences (HRSC, HAAS) (Zhengzhou, China), and cultured at Sanya Experimental Station for phenotype observation and leaf collection. All the above germplasm and populations were available from HSRC, HAAS.

Young leaf tissues of all the above materials were harvested, immersed in liquid nitrogen, and frozen at − 80 °C for genomic DNA extraction. For internode length trait assay, the average internode length of mature plantlet was calculated according to the capsule stem length and the internode number.

Histological analysis of mutant *dw607* and the wild type

In order to explore the stem tissue structure of *dwf1* and wt type, the 6- and 16-day-old seedlings of *dw607* and Yuzhi 11, respectively, were cultured in growth chamber. The fresh stem segments of each sample were collected and immediately fixed in formalin–glacial acetic acid–alcohol (FAA) solution containing 3.8% formalin, glacial acetic acid, and 70% alcohol (V:V:V = 1:1:18) for 24 h. During fixing, the air was extracted through a pump.

The paraffin sections were prepared according to the method of Zhang et al. (2018). The samples were dehydrated with a series of ethanol and stained with 1% safranin. After embedded in paraffin, all the cross sections (10 μm) were cut and stained with 0.1% fast green. The specimens were observed, and the images were photographed under the Leica DM6000 microscope (Leica, Germany) equipped a cooled CCD500 camera (SPOT, Diagnostic Instruments, USA). Images were optimized in Adobe Photoshop 7.0 (Adobe, USA).

Evaluation of endogenous GA_3 amount in *dw607* and the wild type

ELISA assay was applied to evaluate the contents of gibberellic acid (GA_3), indole-3-acetic acid (IAA), abscisic acid (ABA), and brassinosteroid (BR) in sesame samples. Samples of root tip, leaf, and shoot tip of *dw607* and Yuzhi 11 were collected in every 5 days after 18 DAS (days after sowing) and immersed in liquid nitrogen. ELISA test kits for plant hormone essay were developed and supplied by Crop Chemistry Control Research Center, China Agricultural University. Endogenous GA_3, IAA, ABA, and BR in samples were individually extracted according to the procedures of the ELISA test kit manufacture instruction. Three biological replicates were set for each treatment. Each sample was measured with triple replicates.

Genomic DNA extraction, library construction, and Illumina sequencing

Genomic DNA of each sample was extracted using DNeasy Plant Mini Kits (QIAGEN, Hilden, Germany) and fragmented by sonication. Paired-end (PE) libraries were constructed according to Illumina sequencing preparation guidelines. Illumina HiSeq2500 platform (Illumina, San Diego, USA) was applied for genome re-sequencing according to the procedures of Zhang et al. (2016).

Sequencing data analysis and candidate SNP detection

All obtained raw reads of the genome re-sequencing population were filtered using Trimmomatic 0.33 (Bolger et al. 2014). Data alignment to the reference sesame genome was carried out using BWA 0.7.15 (Li and Durbin 2009). Putative SNPs and InDels of 115 individuals were screened using Genome Analysis Tool Kit (GATK3.7) packages (Poplin et al. 2017). All the variants from all the 115 sequencing samples were filtered by the criteria of minimal variant count ≥ 100 and minimum frequency of 0.1. The fine sesame genome (var. Yuzhi 11) (version 2.0) was applied as the reference genome in this study (Zhang et al. 2016). The chromosome position of target gene was determined according to the integration of genome assembly data (version 2.0) and the chromosome annotation information (Zhang et al. 2016; Zhao et al. 2018).

Association analysis and candidate gene location

TASSELE 5.0 and GLM (general linear model) model were used to perform association analysis of all the variants with the phenotype data of the internode length trait for the RIL population. Target gene locus was determined according to the specific interval with the lowest P value. Home-made scripts were applied to screen candidate variants according to the procedures of Zhang et al. (2018). Two groups of sesame variant database, i.e., genomic variant data of 824 sesame accessions (wt) (target region data shown in Supplementary Table 3) and SNP/InDel database of *dwf1* and wt population BSA pools (Supplementary Table 5), were applied to screen candidate variants.

PCR-based SNP markers were designed according to the candidate SNP locus using Primer Premier 5.0 program (https://www.premierbiosoft.com/prierdesign/index.html). PCR was carried out on a PTC-225 machine (MJ Research, Waltham, MA) according to the description of Wei et al. (2014). All the PCR products were electrophoresed in 8% non-denaturing polyacrylamide gels for SNP validation (Liang et al. 2008).

Cloning and annotation of *Sidwf1* gene

To obtain the full gDNA and cDNA sequences of *Sidwf1* alleles in sesame, the primer pairs were designed using Primer Premier 5.0 (Supplementary Table 7). DNA amplification was performed on a PTC-225 machine (MJ Research, USA) (Zhang et al. 2018). Sanger sequencing with three replications was applied. BLASTP and BLAST2GO were carried out to explore the non-redundant (NR) protein and KEGG (Kyoto Encyclopedia of Genes and Genomes) annotations (https://www.genome.jp/kegg/pathway.html) of the target gene.

RNA extraction and expression profile assay of *Sidwf1* gene

Total RNA was extracted from tissues using TriZOL Reagent (Ambion, Life Technologies, USA). The primer pairs of *Sidwf1* gene alleles for quantitative real-time PCR (qRT-PCR) analyses were designed using Primer Premier 5.0 program (https://www.premierbiosoft.com/prierdesign/index.html). Real-time PCR was performed on a Mastercycler-realplex (Eppendorf, Germany) according to the standard method of Zhang et al. (2018). Endogenous reference gene *Siβ-tubulin* was applied for qPCR assay (Wei et al. 2013). Transcript amount of *SiDWF1* gene alleles was normalized against the *β-tubulin* gene and compared using $\Delta\Delta$Ct method according to the method of Wei et al. (2013).

Sidwf1 homolog detection and phylogenetic analysis

Sidwf1 homolog(s) was screened from sesame reference genome (var. Yuzhi 11) using BLASTP. Alignment of amino acid sequences of *SiDWF1* and *Sidwf1* with the homologs of other crops was carried out using DNAMAN (https://www.lynnon.com/pc/framepc.html). All the 20 GID1B homologs of *Erythranthe guttata*, *Ricinus communis*, *Vitis vinifera*, *Nicotiana tabacum*, *Solanum lycopersicum*, *Arabidopsis thaliana*, *Glycine max*, *Prunus persica*, *Gossypium hirsutum*, *Brassica napus*, *Triticum aestivum*, *Zea mays*, and *Oryza sativa* were downloaded from NCBI dataset. MEGA 5.2 was applied to perform sequence comparison and phylogenetic tree construction of *SiDWF1* and homologs [49] (Tamura et al. 2011).

Results

Phenotypic comparison of the dwarf mutant *dw607* and the wild type

In order to explore the dwarf mutagenesis mechanism in sesame, we firstly investigated and compared the 9 key agronomic traits (i.e., plant height, first capsule position, tip length, capsule node number, average internode length, capsule length, capsule width, thousand seed weight, and oil content) of the dwarf mutant *dw607* and Yuzhi 11 (wild type) under standard cultivation conditions in 2012–2014

Table 1 Comparison of key agronomic traits of *dw607* and Yuzhi 11

Material name	Key agronomic traits at mature stage								
	Plant height (cm)	First capsule position (cm)	Tip length (cm)	Capsule node number	Average internode length (cm)	Capsule length (cm)	Capsule width (cm)	Thousand seed weight (g)	Oil content (%)
*dw*607 (*dwf1*)	118.25 ± 8.85**	16.50 ± 3.51	5.50 ± 2.08	22.75 ± 5.44	4.31 ± 0.50**	3.36 ± 0.15	0.96 ± 0.05	3.263 ± 0.13**	52.61% ± 0.07
Yuzhi 11 (wt)	176.00 ± 4.97	23.00 ± 4.83	4.75 ± 3.30	21.75 ± 0.50	6.82 ± 0.06	3.64 ± 0.12	0.98 ± 0.06	2.697 ± 0.12	51.06% ± 0.14

The data are the investigation results collected at Hainan Experimental Station in 2013

* and ** refer to the significant correlation under the levels of 0.05 and 0.01, respectively

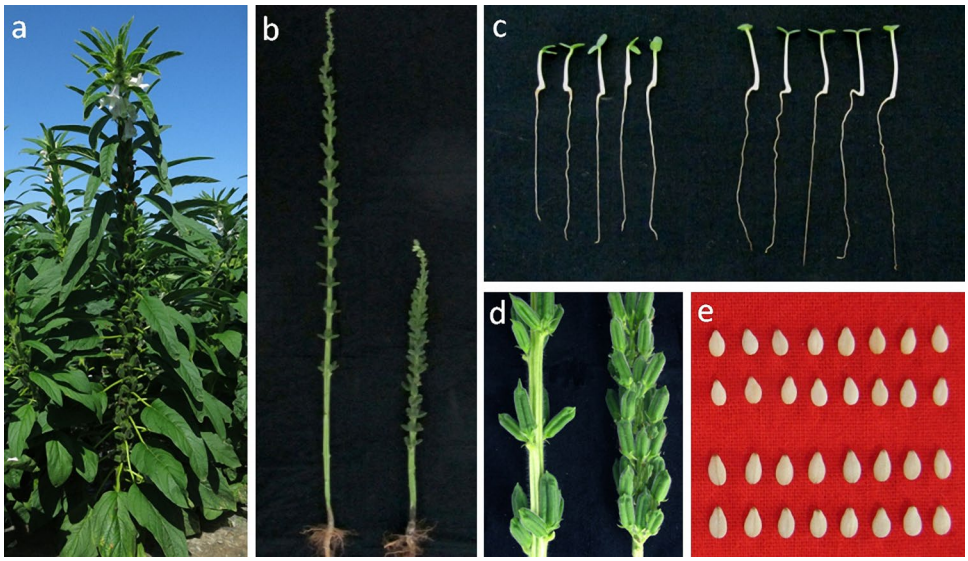

Fig.1 Phenotypic comparison of dwarf mutant *dw607* with short internode and the wild type Yuzhi 11. **a** Plant morphology of *dw607* at late flowering stage; **b** plant height and capsule stem length comparison of Yuzhi 11 (left) and *dw607* (right) at mature stage; **c** seedling comparison of *dw607* (left) and Yuzhi 11 (right) for 3 days after germination; **d** internode length comparison of Yuzhi 11 (left) and *dw607* (right); **e** seed size comparison of the wild type (upper two lows) and *dw607* (lower two rows)

(Table 1; Fig. 1). For *dw607*, the phenotypic characters of root, leaf, stem, capsule, seed, and other organs differed from the wild type (Fig. 1). The stem of *dw607* during germination (Fig. 1c) to flowering stages (Fig. 1b) grew shorter than that of the wild type. Compared with Yuzhi 11 (wt) during mature stage, the plant height of *dw607* (*dwf1*) significantly declined from 176.00 to 118.25 cm, and the internode length reduced from 6.82 to 4.31 cm ($P < 0.01$). Meanwhile, the thousand seed weight (TSW) also significantly increased ($P < 0.01$). Correlation analysis indicted that both internode length and thousand seed weight were significantly affected by plant height trait (Table 1). Correspondingly, we evaluated the difference of plant height between *dw607* and Yuzhi 11 during the cycle life (Supplementary Fig. 1) (Supplementary Table 1). Results showed that the plant height of *dw607* plantlets increased slowly at seedling stage (1–28 days after sowing, DAS). In early flowering and flowering stages (34–63 DAS), the plant height gap between dw607 and Yuzhi 11 was getting more evident (Supplementary Fig. 1). As to the growth rhythm, the initiation of flowering period in *dw607* delayed about 5 days, and the whole life period prolonged 7 days (Supplementary Table 1).

Subsequently, we performed the cytological character analysis of *dw607* and Yuzhi 11 (Fig. 2). Transverse and vertical sections of stems of 6-day-old and 16-day-old seedlings were observed and compared. For 6-day-old *dwarf 607* and Yuzhi 11 seedlings, the cell length and width of vertical hypocotyl section were about 80.9 μm and 40.0 μm and 148.1 μm (*) ($P < 0.05$) and 38.84 μm, respectively. Interestingly, for 16-day-old *dw607* and Yuzhi 11 seedlings, the cell length and width of vertical parenchyma tissue section were about 33.4 μm and 37.7 μm and 102.4 μm (*) and 67.4 μm (*), respectively. The difference in cell length and width of parenchyma tissue (Pc) and pith (Pi) between dwarf mutant and the wild type was more evident (Fig. 2a–h). Thus, the vascular bundle cells (VC) and Pc tissue of *dw607* arranged much tighter, and the xylem tissue became thicker than the wild type (Fig. 2g, h).

Inheritance analysis of dwarf mutation with short internode length trait

Sesame is a crop with indefinite inflorescence. Plant height, as well as the stem length trait, is affected by the development of inflorescence meristem and flowering period in sesame. For *dw607*, 'plant height' and 'internode length' traits are significantly associated with the dwarf phenotype (Table 1). Then, we chose the internode length trait to explore the inheritance of dwarfing mutation. We firstly performed the cross-combination of '*dw607* (*dwf1*) and 15N41 (wt type)' and '*dw607* (*dwf1*) and Yuzhi 11 (wt type)' for target trait inheritance analysis (Table 2). For the F_1 and F_2 population derived from the cross '*dw607* (*dwf1*) × Yuzhi 11 (wt type),' the average internode length of *dw607* (P_1) and Yuzhi 11 (P_2) was 4.0 cm and 6.1 cm, respectively (Fig. 3). The average internode length of F_1 individuals was high (6.0 cm) and similar to that of normal genotype. Meanwhile, the internode length of F_2 individuals continuously varied from 2.5 to 10.0 cm with the peak number of 6.5–7.0 cm. In order to accurately determine the phenotype segregation ratio of each F_2 population, the individuals with internode length of ≤ 5.0 cm (close to the value of P_1 (*dwf1*)) were referred to '*dwf1* type,' while the others with the internode length of more than 5.0 cm (close to the value of P_2 (wt)) were 'wild type.'

In the two combinations between *dwf1* and normal genotype, the backcrosses (BC_2) developed from F_1 and wt type displayed the normal internode length (Table 2). The

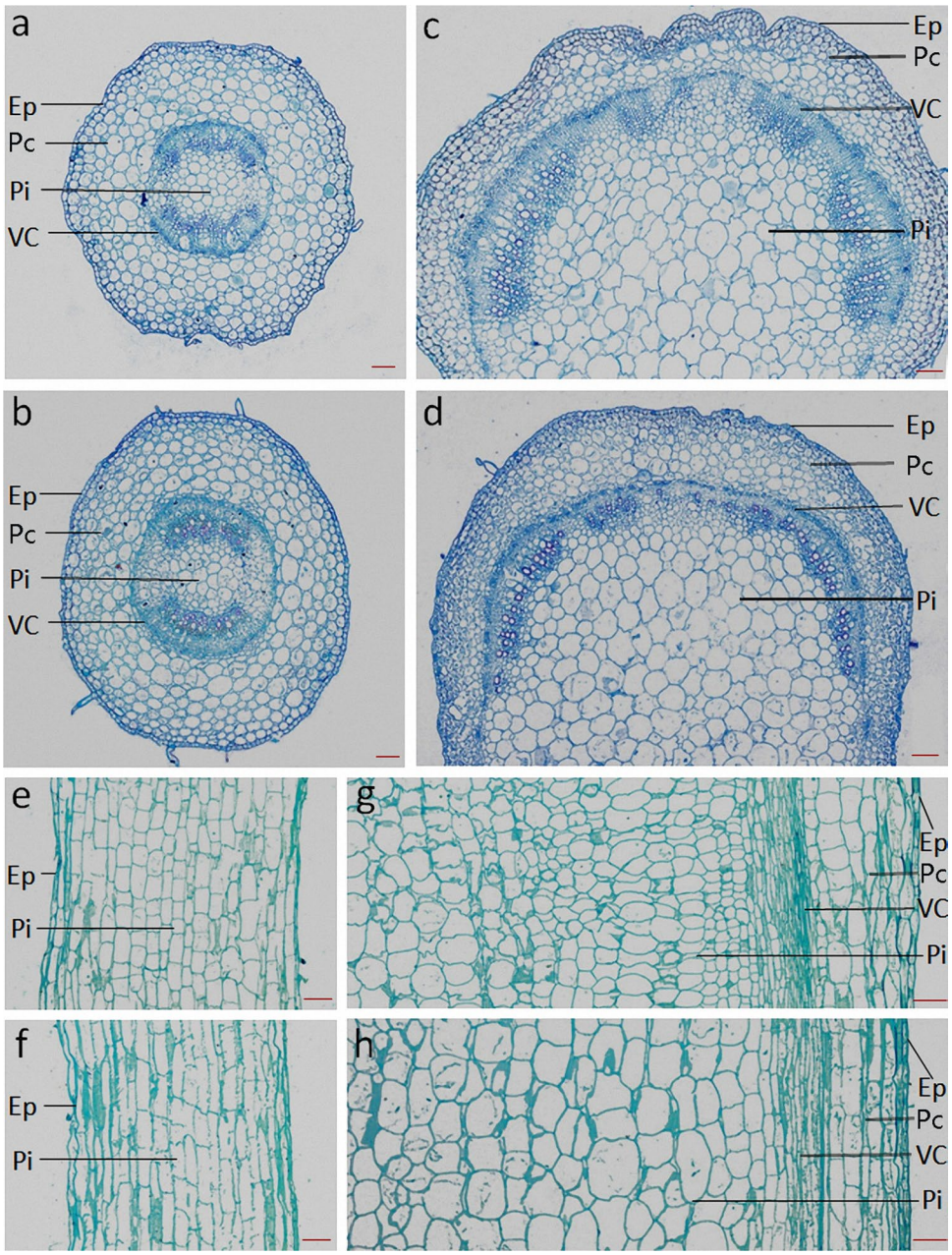

Fig. 2 Cross section of stem organ of *dw607* and Yuzhi 11. **a** and **b** Transverse stem section of 6-day-old seedlings of *dw607* and Yuzhi 11, respectively; **c** and **d** transverse stem section of 16-day-old seedlings of *dw607* and Yuzhi 11, respectively; **e** and **f** vertical stem section of 6-day-old seedlings of *dw607* and Yuzhi 11, respectively; **g** and **h** vertical stem section of 16-day-old seedlings of *dw607* and Yuzhi 11, respectively. *Ep* epidermis; *Pc* parenchyma tissue; *Pi* pith; phloem; *VC* vascular bundle cell. Red bar = 100 μm (color figure online)

Table 2 Inheritance analysis of the *DW* and *dwf1* genotypes in sesame

Cross combination		Normal genotype no. /*dwf1* genotype no.*				Expected ratio	
Parent 1 (*dwf1*)	Parent 2 (wt)	F_1	BC_1 (χ^2 value)	BC_2	F_2 (χ^2 value)	BC_1	F_2
dw607	15N41	281/0	78/72 (0.1667)	110 /0	132/48 (0.1852)	1:1	3:1
dw607	Yuzhi 11	260/0	188/198 (0.2098)	245/0	202/61 (0.3663)	1:1	3:1

$\chi^2_{(0.05,\,1)} = 3.84$

*The internode length standard for differentiating the dwarf and the wild type is set at 5.0 cm in this study

segregation ratio of *dwf1* backcrosses (BC_1) and F_2 populations between the short internode length (*dwf1*) and the normal phenotype (wt) fitted the expected ratios of 1 (*dwf1*): 1 (wt) ratio and 3 (*wt*): 1 (*dwf1*), respectively. Further, Chi-squared tests ($P > 0.05$) confirmed that the segregation of the short internode length trait in sesame fitted the Mendelian

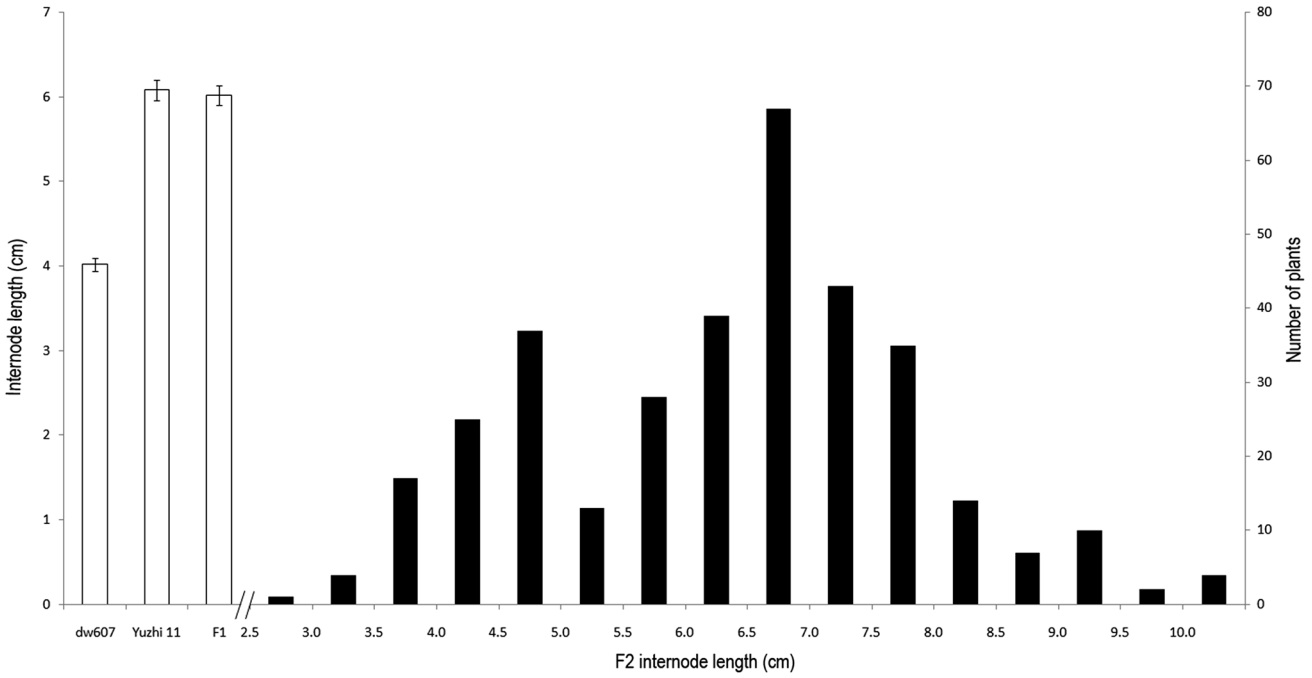

Fig. 3 Distribution of the internode length value in F_2 population of the cross '*dw607* (*dwf1*) × Yuzhi 11 (wt type).' Left vertical axis indicates the values of internode length trait of two parents and F1 population. Right vertical axis indicates the number of F_2 individuals with specific internode length

inheritance mode. The dwarf mutation with short internode length trait is controlled by a recessive gene allele in sesame. Here the dwarf mutation locus in mutant *dw607* and the normal allele in Yuzhi 11 were annotated as *Sidwf1* and *SiDWF1*, respectively.

Location of *Sidwf1* gene using association mapping and genome variants screening

To locate the target gene locus related to the short internode length and dwarf trait, we firstly performed the cross-population association mapping using a RIL population of the cross '*dw607* (*dwf1*) × 15N41 (wt type)' with 831 F_6 individuals. The two parents (*dw607* and 15N41) and the 113 F_6 individuals of the RIL population were re-sequenced using Illumina sequencing platform (Table 3). In total, 748.13 Gb of raw data of the 115 samples was obtained. The average genome coverage was 18.3-fold per sample. All mapped reads were aligned to the sesame reference genome (var. Yuzhi 11, PRJNA315784) for SNP calling. A total of 780,199 unique SNPs were found in the two parents.

Subsequently, all the 780,199 unique SNPs were applied for variants screening in the 113 individuals of the RIL population. After filtered, 496,486 SNP/InDel variants were detected for Joint calling. According to the reference sesame genome (Yuzhi 11) and the nomination of sesame

Table 3 Genome sequencing information of the mapping population for internode length trait

Sample name	Raw read number	Coverage (×)[a]	Ratio of high-quality reads		Variant loci number	Unique loci[c]
			$Q \geq 20$	$Q \geq 30$		
dw607 (*dw*) (P_1)	49,096,366	20.80	96.55	92.46	372,152	205,941
15N41 (wt) (P_2)	51,985,512	22.03	96.60	92.50	740,469	574,258
113 F_6 progeny[b]	4,886,483,600	18.32	96.65	91.32	–	–
Total	4,987,565,478	18.38	96.65	91.34	–	–

[a]The genome coverage is calculated based on the sesame genome size of 354 Mb estimated by K-mer (Zhang et al. 2013)

[b]For the genome sequences of 113 F_6 progeny, the genome coverage per progeny is 18.32-fold

[c]Unique variants existed in a parent after compared with the other parent

chromosome set (Zhang et al. 2018; Zhao et al. 2018), a total of 423,138 SNP/InDel variants were plotted on the 13 chromosomes (Fig. 4). Association mapping results showed that the variant site (C9_7086504) with the lowest of P value (2.59E−15) located on Contig C9.scaffold2 of *Si*Chr.4. To screen the target variants from the target contig, we chose the up- and downstream 200-Kb flanking sequences of C9_7086504 as the target interval linked to the short internode length trait (*dwf1*).

The interval C9 between C9_6861138 and C9_7285379 markers contained 58 variants with the P value variation of 9.08E−05 to 2.59E−15 (Supplementary Table 2). Then, we filtered these detected 58 SNP/InDel variants using the regional genome variants data of 824 sesame accessions (wild type). For the 824 accessions, 8,985 SNPs/InDels existed in the region of C9_6861138 and C9_7285379 (Supplementary Table 3). Genomic variants screening results showed that 12 variant loci (green dots in Fig. 4) were retained in the target interval for the population (Supplementary Table 4). Furthermore, we screened the above plotted variant sites using the genome data of two BSA pools of dwarf type (*dwf1*) and wild type (wt) of the F_{2-3} population (uploaded to NCBI dataset) (Supplementary Table 5). As a result, 5 SNP/InDel sites, i.e., C9_6958525, C9_6986819, C9_6989486, C9_7080799, and C9_7225874, were retained in the target interval (Supplementary Table 6).

Interestingly, differing from the other 4 variants distributed in intergenic regions, a SNP C9_6989486 is located in gene coding region (C9.scaffold2.572) and caused the missense mutation from C to T in C9.scaffold2.572. To confirm this SNP site in *dwf1* genotype, we designed the primer pair of *SiSNPdwf1* (Supplementary Table 7) and screened the test population including 600 F_{2-3} individuals of test population and 500 sesame germplasm accessions with normal internode length (Supplementary Fig. 2). PCR screening results proved that the *SiSNPdwf1* alleles in gene C9.scaffold2.572 entirely accorded with the phenotype segregation in the test population. Then, C9.scaffold2.572 gene was regarded as the target gene controlling the short internode length and dwarf trait in *dw607* and was named *Sidwf1*.

Structure analysis of *SiDWF1* gene and homolog in sesame

With the aid of the reference genome information of var. Yuzhi 11, we designed the primer pairs and amplified the entire cDNA and DNA sequences of *SiDWF1* (C9.scaffold2.572) allele (Supplementary Table 8). Sanger sequencing and gene alignment results proved that the full sequence length of *SiDWF1* gene (NCBI Accession No. KY649623) in Yuzhi 11 was 1,638 bp and comprised of 2 exons (Fig. 5a). Correspondingly, *SiDWF1* encodes 343 amino acids. For *dw607*, the SNP mutation of C/T occurred in Exon 2 of *Sidwf1* gene (Fig. 5a). The nucleotide C at 1,057-bp position was mutated into T, and the amino acid P_{150} (proline) in the conserved sequence changed into S_{150} (serine) (Fig. 6). Non-redundant (NR) protein annotation results revealed that *SiDWF1* gene was identified to encode a gibberellin receptor GID1B-like protein (Supplementary Table 5).

BlastP analysis indicated that there was a homolog gene, i.e., evm.model.C4.1012 (the same annotated as a gibberellin receptor GID1B-like protein) with SiDWF1 in sesame (Fig. 5b). The homolog evm.model.C4.1012 was 1,574 bp with the gene resemblance of 86.6% to SiDWF1. Herein, this homologous gene evm.model.C4.1012 was named *SiDWF2*. Amino acid sequence comparison indicated that 33 amino acids of SiDWF1 differed from those of SiDWF2 (Fig. 5b). Moreover, we performed the interspecies comparative analyses of 22 SiDWF1 homologs in 14 crops (partial results in Fig. 6). The results showed that SiDWF1 had the high resemblance to the GID1B homologs from the other 13 species, as the resemblance rate varied from 60.2% (TaGID1-D1 and ZmGID1) to 88.0% (EgGID1b) (Fig. 7). Compared with the 20 GID1B homologs in 13 plant species with normal internode length phenotype, Sidwf1 protein carried the specific amino acid mutation of Pro/Ser in the

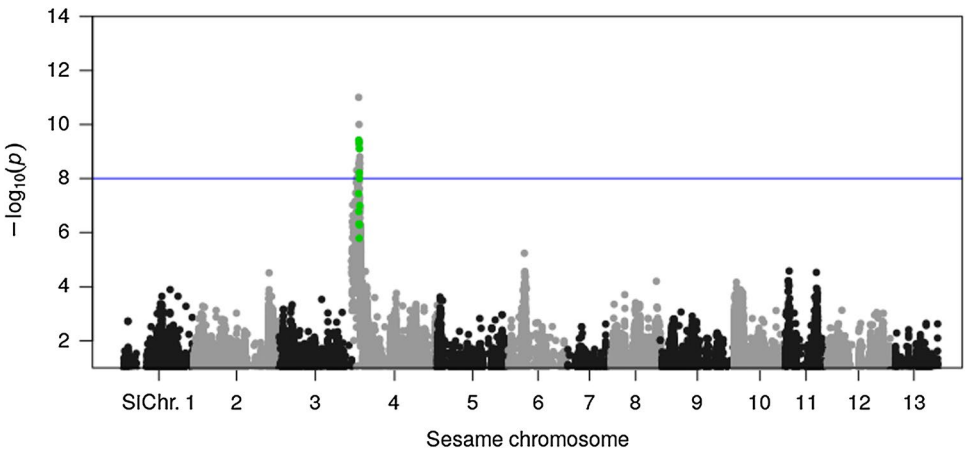

Fig. 4 Cross-population association mapping of *Sidwf1* gene locus in sesame. Manhattan plot of SNP/InDel association mapping of the short internode trait is performed using a RIL population. The peak of − log 10 (P) is located on *Si*Chr. 4. After screened using the genome variants data, 12 variants (green dots) are retained as the candidate markers associated with the short internode length trait in sesame. Blue line indicates the *P* value of E−8 (color figure online)

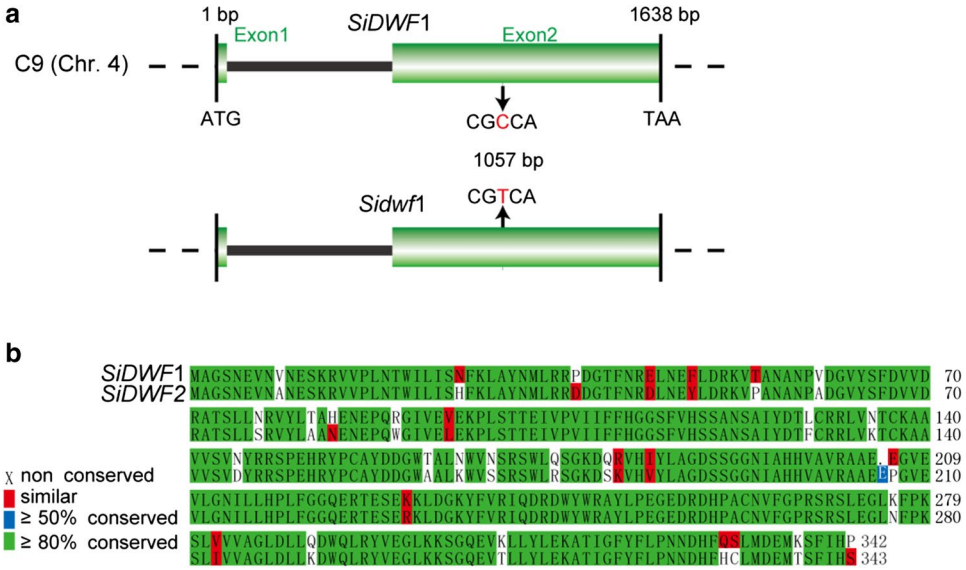

Fig. 5 Sequence and structure comparison of *SiDWF1* and the homology. Gene structure of *SiDWF1* gene and the allele *Sidwf1* homologs. **a** Structure of *SiDWF1* and the allele *Sidwf1*. **b** Comparison of *SiDWF1* and the homolog *SiDWF2*

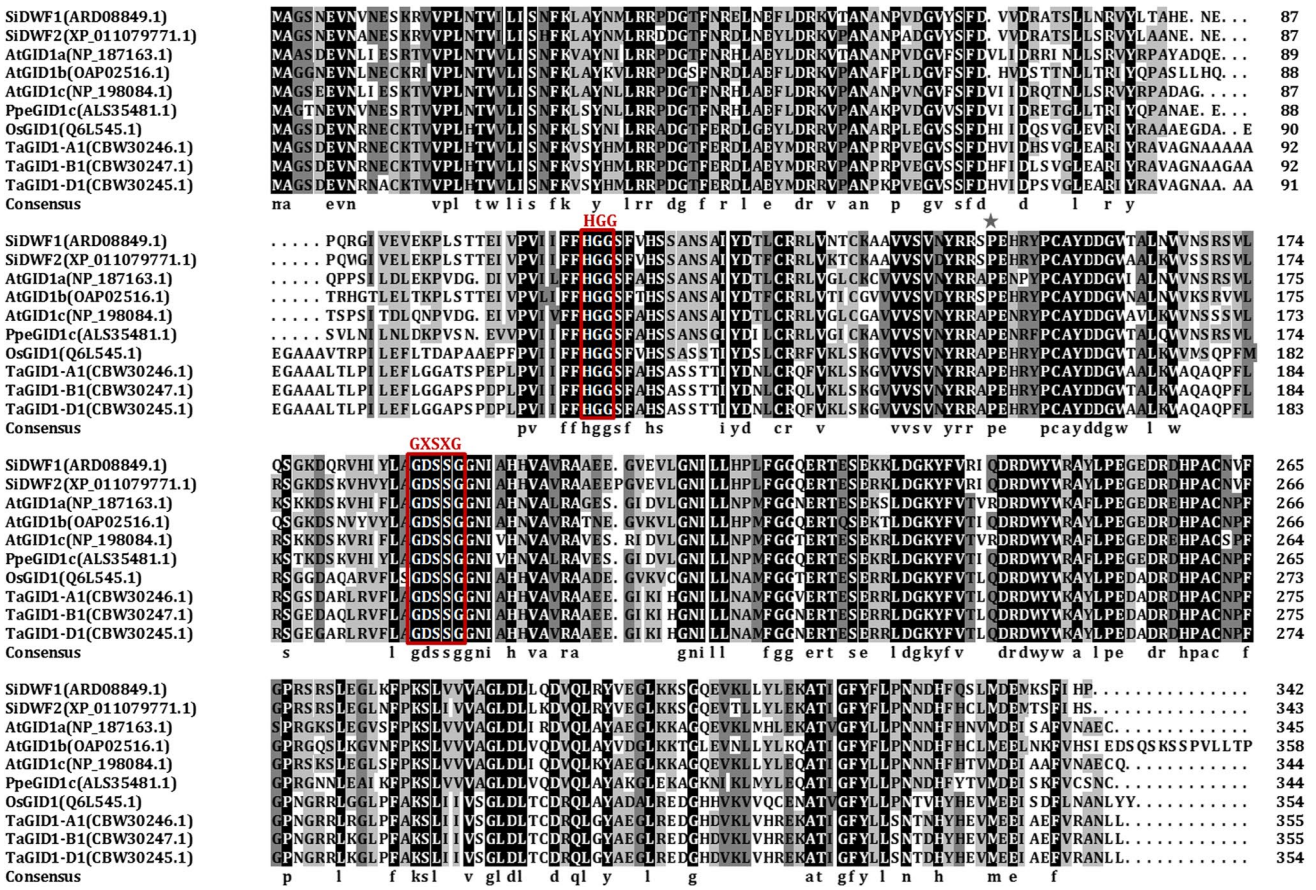

Fig. 6 Protein sequence comparison of *SiDWF1* and homologs in sesame and other plant species. Eight ortholog proteins homologous to SiDWF1 (ARD08849.1) and SiDWF2 (XP_011079771.1) are AtGID1a (NP 187163.1), AtGID1b (OAP02516.1), and AtGID1c (NP 198084.1) in *Arabidopsis thaliana*, PpeGID1c (ALS35481.1) in *Prunus persica*, TaGID1-A1 (CBW30246.1), TaGID1-B1 (CBW30247.1), and TaGID1-D1 (CBW30245.1) in *Triticum aestivum*, OsGID1 (Q6L545.1) in *Oryza sativa*. Identical residues are shaded in black; conserved residues are shaded in gray; and residues with low identity are shaded in light gray. The black dot indicates amino acid gap. Asterisk indicates the mutation site of *SiDWF1* to *Sidwf1* protein in highly conserved region. Conserved bases in red frames are HGG and GXSXG motifs, which exist in hormone-sensitive lipase (HSL) family,

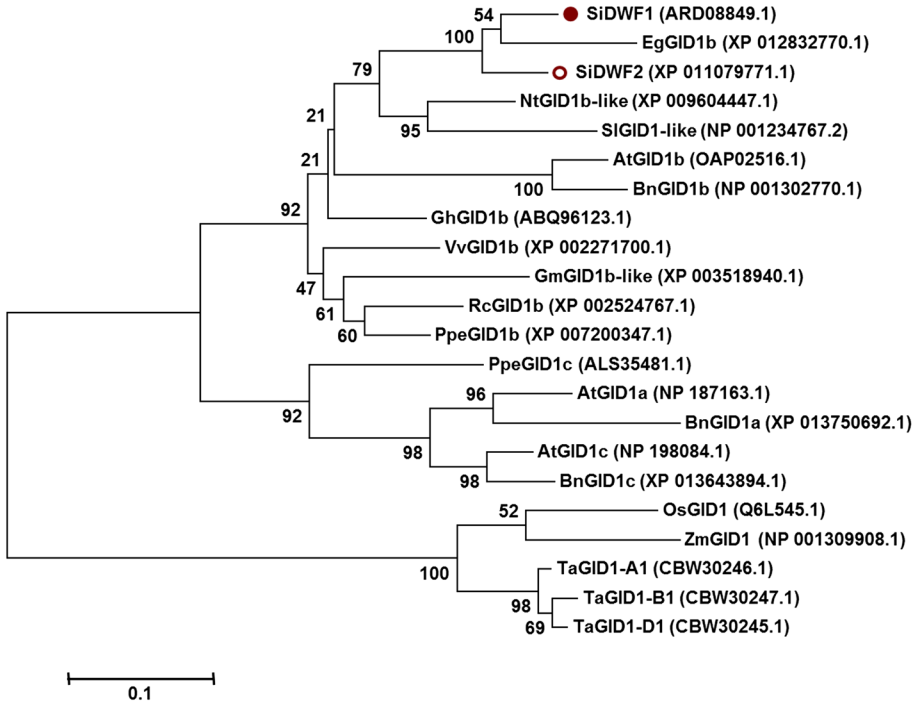

Fig. 7 Phylogeny analyses of SiGID1B protein in sesame and other plants. Data above the branches indicate the support with 1000 bootstrap replications. The cluster includes SiDWF1 and SiDWF2 in *Sesamum indicum* and 20 homologs in 13 plants, i.e., EgGID1b (XP 012832770.1) in *Erythranthe guttata*, RcGID1b (XP 002524767.1) in *Ricinus communis*, VvGID1b (XP 002271700.1) in *Vitis vinifera*, NtGID1b-like (XP 009604447.1) in *Nicotiana tabacum*, SlGID1b-like (NP 001234767.2) in *Solanum lycopersicum*, AtGID1a (NP 187163.1), AtGID1b (OAP02516.1), and AtGID1c (NP 198084.1) in *Arabidopsis thaliana*, GmSlGID1b-like (XP 003518940.1) in *Glycine max*, PpeGID1b (XP 007200347.1) and PpeGID1c (ALS35481.1) in *Prunus persica*, GhGID1b (ABQ96123.1) in *Gossypium hirsutum*, BnGID1a (XP 013750692.1), BnGID1b (NP 001302770.1), and BnGID1c (XP 013643894.1) in *Brassica napus*, TaGID1-A1 (CBW30246.1), TaGID1-B1 (CBW30247.1), and TaGID1-D1 (CBW30245.1) in *Triticum aestivum*, ZmGID1 (NP 001309908.1) in *Zea mays*, and OsGID1 (Q6L545.1) in *Oryza sativa*

conserved sequence. Of the 22 homologs, EgGID1b (XP 012832770.1) in *Erythranthe guttata* displayed the closest relationship with SiDWF1.

Expression profiles of *SiDWF1* alleles and dynamic GA_3 variation in sesame

To reveal the expression profiles of *SiDWF1* alleles in *dwf1* and wild type, we monitored the transcription level of *SiDWF1* and *Sidwf1* in root, leaf, stem, bud, and capsule tissues of Yuzhi 11 and *Dw607*, respectively, using real-time quantitative PCR (RT-qPCR) (Fig. 8). The results displayed that *SiDWF1* and *Sidwf1* genes highly expressed in most tissues (i.e., root, stem, leaf, shoot, bud, and 0-d capsule) except for 5-d-old capsule pericarp and seed. The highest relative expression level (1/2△△CT) of *dw607* and Yuzhi 11 occurred in bud tissue with the peak value of 2.6 and 2.1, respectively. Compared with *SiDWF1*, *Sidwf1* expressed significantly higher in leaves and buds of mutant *dw607*.

As GID1B proteins take part in the GA biosynthesis pathway and promote the GA-responsive growth, we also monitored the content variation in endogenous hormones of GA_3, IAA, ABA (abscisic acid), and BR in Yuzhi 11 and mutant *dw607*, respectively (Supplementary Fig. 3). The results displayed that the amount of endogenous GA_3 per gram tissue varied from 4–22 μg in *dw607* during the life cycle. From seedling stage to late flowering stage, GA_3 content in shoot, root, and leaf tissues fluctuated. Meanwhile, a highlighted tendency presented in leaf organ (Supplementary Fig. 3a-c). Compared with the wild type, the level of endogenous GA_3 in *dw607* leaf varied with time lag. In shoot and root tip, the GA_3 accumulation variation between *dw607* and Yuzhi 11 presented with the same tendency.

In addition, the accumulations of IAA, ABA, and BR in *dw607* and Yuzhi 11, respectively, were compared. For IAA, the variation tendency in d*w607* and Yuzhi 11 was similar. The peak amount of IAA always occurred in shoot tip and leaf at flowering stage (Supplementary Fig. 3d-f). The IAA content in root tip maintained lower than those of leaf and shoot tip. Meanwhile, comparison results indicated that the ABA level and variation tendency in *dw607* were similar to those of Yuzhi 11, even though the ABA content in some samples of Yuzhi 11 changed violently (Supplementary Fig. 3g-i). During flowering stage, the peak amount of

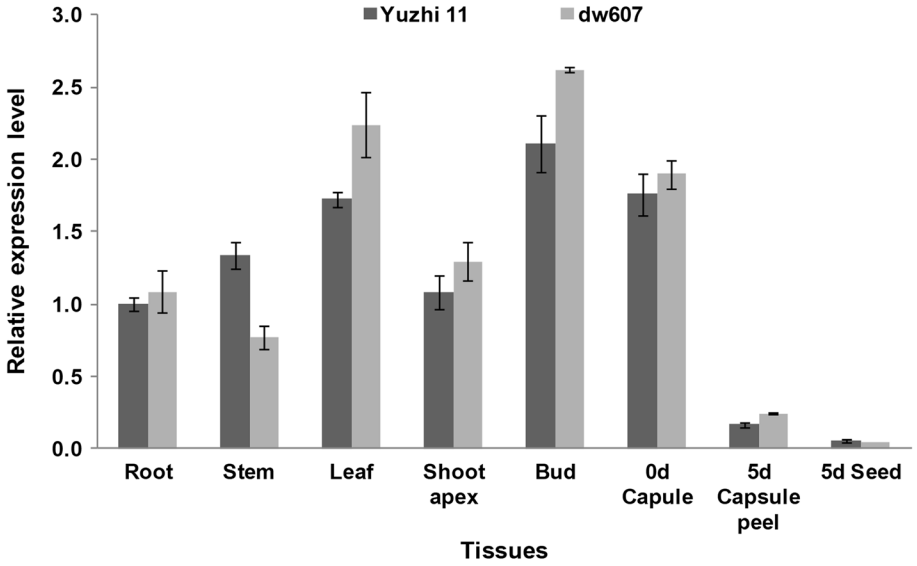

Fig. 8 Expression profiles of *SiDWF1* gene alleles in Yuzhi 11 and *dw607*, respectively. The tissues of root, stem, leaf, bud, 0-d capsule (0-d c), 5-d capsule pericarp (5-d cp), and 5-d seed (5-d s) are collected from plantlets of Yuzhi 11 and Dw607 at flowering stage. Gene expression of each tissue is measured with triple biological replications

ABA in shoot tips of Yuzhi 11 and *dw607* was 140.3 μg g^{-1} and 149.8 μg g^{-1}, respectively. As for BR content, the evaluation results showed that the peak content of BR in shoot, root, and leaf tissues of *dw607* delayed, while the variation tendency between *dw607* and Yuzhi 11 was similar (Supplementary Fig. 3j-l).

Discussion

Plant height affects plant architecture, lodging resistance, yield, and even harvest style for crops. For sesame, to reduce the plant height and concurrently increase the seed yield and the adaption for harvest mechanization is one of the key breeding objectives. In 2009, the dwarf sesame mutant *dw607* with short internode length and high seed weight traits was created by EMS mutagenesis (Wang et al. 2017a). For the dwarf mutant, the plant height and internode length decline about 50%. The yield per plantlet and thousand seed weight increase, even though the capsule node number and capsule number per plant were not affected. Notably, the first dwarf sesame variety Yuzhi Dw607 (China variety authorization no. CNA013391E) was bred from the mutant *dw607* and applied for sesame production in China since 2015. The highest yield level of var. Yuzhi Dw607 touched more than 3300 kg per ha in Xinjiang production region of China in 2017 (data not shown) and displays the high yield potential. Similar to the first determinate variety Yuzhi DS899, the dwarf variety Yuzhi Dw607 represents the outstanding varieties in recent sesame breeding history (Zhang et al. 2019).

In this study, the morphological and genetic analysis of *dw607* was systematically performed. The target gene, *Sidwf1* controlling the plant height and internode length traits, was cloned, based on the combination strategy of cross-population association mapping and genomic variants screening. The results proved that the above gene cloning method is highly efficient and convenient for quality trait-related genetics research in sesame (Zhang et al. 2018). For *dw607*, the development characters of stem and plant architecture are affected by the mutation of *SiDWF1* gene alleles, which encodes a GID1B-like protein with HGG and GXSXG motifs (Fig. 6). Till now, GID1 receptor genes have been characterized in *Arabidopsis thaliana*, ferns, cotton, maize, barley, oilseed rape, wheat, and other plants (Griffiths et al. 2006; Hirano et al. 2007; Aleman et al. 2008; Chandler et al. 2008; Suzuki et al. 2009; Zeng et al. 2011; Li et al. 2013). Different from other homologs in other crops, *Sidwf1* gene contained the only missense change of SNP C_{1057}, which was mutagenized to T_{1057} and resulted in the amino acid change of P_{150} (proline) to S_{150} (serine) (Fig. 5). In plants, GID1B-like proteins are conservative. Compared to the homologs of monocotyledonous crops, the resemblance rate of SiDWF1 is still high to 60% (Fig. 7).

The GID1 receptor gene was initially identified in rice (*OsGID1*), which is involved in gibberellin biosynthesis pathway (Ueguchi-Tanaka et al. 2005). In a plant species, GID1B or GID1B-like proteins always have one or more homologs which reveal the sequence conservation and the complexity of gibberellin biosynthesis pathway and regulation. In wheat, both of the homologous DELLA genes Rht-B1 and Rht-D1 cause dwarfing (Peng et al. 1999). For sesame, two ortholog genes (i.e., *SiDWF1* and *SiDWF2*) were proved to encode GID1B-like proteins (Fig. 6). A SNP mutation (C1057T) of *SiDWF1* caused the short internode length in *dw607*. Thus, we inferred that *SiDWF2* might take different functions from *SiDWF1*. In addition, compared with the wild type, the development rhythm of plant architecture in

dw607 delayed. Mutagenesis of the conserved domain of *SiDWF2* might also cause the architecture change in sesame.

Till now, hundreds of dwarf mutants have been found in many species. Most of these mutations are involved in the biosynthesis and signal transduction of the GA_3, BR, or other plant hormones (Chen et al. 2017; Yan et al. 2017). In this study, the sesame dwarf mutant *dw607* also exhibited the change of stem development process. The internode length and stem length were significantly reduced (Table 1). Similar to *emf2b* in rice (Zhong et al. 2018) and *m34* in maize (Li et al. 2018a), cell expansion of stem tissue in *dw607* was seriously inhibited (Fig. 2). Moreover, evaluation results of GA_3, IAA, ABA, and BR content reflected that the accumulation pattern of the four endogenous hormones in *dw607* and the wild type was similar (Supplementary Fig. 3). The variation in GA_3 content in root, leaf, and shoot tissues of dwarfing mutant presented the delayed rhythm, consistent with the growth and development styles of *dw607* (Supplementary Fig. 3; Table 1). SiDWF1 belongs to gibberellin-insensitive protein. Theoretically, the dwarfing mutation of *dwf1* type cannot be entirely restored even with the artificial regulation at specific stage (Ashikari et al. 1999). Further GA_3 complement experiment proved that the dwarfing trait of *dw607* could not be recovered under the artificial supplement of GA_3 (data not shown). Thus, the dwarfing type of *dw607* is similar to that of the gibberellin-insensitive rice mutant *dwarf 1* (*d1*) (Ashikari et al. 1999).

In soybean, Gazara et al. (2018) found a GID1b homolog (*Gmax.GID1b3*) expressed highly in roots and nodules, as well as in flowers. Similarly, we detected that the transcripts of *Sidwf1* gene were highly expressed in root, leaf, stem, buds, and 0-d capsule tissues (Fig. 8). Moreover, the main tissues and stages with high expression of *SiDWF1* alleles also accumulated more GA_3, which would reflect the inner relationship of the dwarfing gene and the main biological process regulation. The findings supply the foundation for elucidating the regulation of the molecular mechanism on the short internode length and dwarf trait in sesame. The developed SNP marker for *Sidwf1* also improves the development of molecular breeding in sesame.

Conclusion

The short internode length and dwarfing trait in mutant *dw607* is controlled by a recessive gene allele (*Sidwf1*). Cell size of stem parenchyma and pith tissues in *dw607* significantly reduce. SiDWF1 is a gibberellin receptor GID1B-like protein. The SNP mutation of C_{1057} to T_{1057} resulted in an amino acid change and affected the gene function of *SiDWF1*. The findings revealed the molecular genetic mechanism of the short internode length and dwarf trait in sesame for the first time.

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Author contribution ZH conceived the technical route and guided the manuscript for publishing. MH guided the experiments, performed the data analysis, and drafted the manuscript. LC and DY conducted the main data analysis and experiments. WL and JM performed the genetic experiments and participated in result validation. All authors read and approved the final manuscript.

Availability of data and materials The cDNA sequence of *SiDWF1* gene was available in NCBI with Accession No. KY649623. The BSA data of the *dwf1* and the wild type were available in NCBI under bioproject PRJNA555174 with SRA Accession No. SRR9733676-SRR9733681.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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