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Combining QTL and candidate gene analysis with phenotypic model to unravel the relationship between lodging and related traits in soybean

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Abstract Lodging is one of the major influencing factors of yield and quality in soybean [*Glycine max* (L.) Merr.] and other crops. To dissect the genetic basis of lodging in soybean, a recombinant inbred line population consisting of 165 lines was used to evaluate lodging percentage and eight related traits (branch number, internode length, number of nodes, plant height, stem diameter, stem strength, root length, and root weight) in three environments. Regression analysis indicated that plant height and root weight, which explain more than 55% of the variation in lodging percentage, might be the key factors influencing lodging in soybean. Nine consensus quantitative trait locus (QTLs) of lodging percentage were detected in one to three environments. Of which, eight consensus QTLs were colocated with 16 consensus QTLs of lodging-related traits by meta-analysis. In addition, seven candidate genes with the biological functions of shoot branching, root development, internode elongation, and lignin biosynthesis were identified on four pleiotropic QTL regions (*oq.13-1*, *oq.13-2*, *oq.19-2*, and *oq.19-3*) for lodging percentage and related traits. These findings showed that the consensus QTLs of lodging percentage might result from the pleiotropic QTLs affecting the lodging-related traits. Soybean lodging is determined by the cumulative effect of many traits/processes of growth and development. The combination of MAS, statistical model, and phenotypic selection will provide a powerful breeding strategy for lodging resistance in soybean.

Keywords Soybean · Lodging · QTL · Meta-analysis · Breeding strategy

Introduction

Lodging, the permanent displacement of stems from the vertical, is one of the major factors limiting yield potential and influencing the quality in many crops, including maize (Farkhari et al. 2013), wheat (Keller et al. 1999; Foulkes et al. 2011), rice (Kashiwagi and Ishimaru 2004; Islam et al. 2007), barley (Berry et al. 2006; Sameri et al. 2009), oats (Pinthus 1973), rapeseed (Islam and Evans 1994), tomato (Adelana 1980), tobacco (Menchey et al. 1993), and soybean (Cooper 1971; Woods and Swearingin 1977; Noor and Caviness 1980; Lee et al.

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1996; Board 2001; Chen et al. 2011). Lodging leads to considerable losses in agricultural production, and it is estimated to cause 15–80% losses of grain (Foulkes et al. 2011) and 11–32% losses of soybean (Woods and Swearingin 1977; Noor and Caviness 1980). Lodging resistance is an important goal in crop breeding, and many studies have tried to find morphological traits that are correlated with lodging and could be used as indirect selection parameters. Several morphological traits, such as plant height (Islam et al. 2007), stem (breaking) strength (Kashiwagi and Ishimaru 2004; Chen et al. 2011), and stem diameter (Kashiwagi et al. 2008), have been proposed as the key factors influencing lodging in recent years. It is shown that morphological traits of plant height (Kashiwagi and Ishimaru 2004; Islam et al. 2007), internode length (Berry et al. 2006; Sameri et al. 2009), stem diameter (Kashiwagi et al. 2008), number of nodes (Chen et al. 2011), branch number (Landi et al. 2007), stem (breaking) strength (Kashiwagi and Ishimaru 2004; Kashiwagi et al. 2008; Chen et al. 2011), root system (Keller et al. 1999; Landi et al. 2007), chemical components of lignin, cellulose (Kashiwagi and Ishimaru 2004; Ma 2009; Wang et al. 2012) and silicon (Ma and Yamaji 2006) in stem, environment of rain and wind (Kashiwagi et al. 2008), field management of fertilization (Crook and Ennos 1995), and control of disease and insect infestation (Pinthus 1973) are the factors influencing lodging in crops. Thus, crop lodging is a complicated phenomenon influenced by many factors from physiology and genetics to field management and environment (Ma 2009).

Meta-analysis was first proposed to integrate and summarize results from separate studies (Glass 1976) and was eventually adopted for genetic and QTL studies (Goffinet and Gerber 2000). QTL meta-analysis is a powerful approach to synthesize information from different experiments involving single or multiple populations; this approach can also evaluate QTL information from multiple environments or traits and refine the position of the QTL with a reduction in the confidence interval (Arcade et al. 2004; Chardon et al. 2004). According to the positions and confidence intervals of the QTLs from different environments and traits, algorithms for QTL meta-analysis were used to estimate the number and positions of the meta-QTL (Goffinet and Gerber 2000; Arcade et al. 2004; Chardon et al. 2004). In many crops, the genetic architecture associated with yield, seed composition, agronomic and physiological traits, and biotic and abiotic stress were unraveled by QTL meta-analysis (Truntzler et al. 2010; Chen et al. 2011; Swamy et al. 2011; Shinozuka et al. 2012; Semagn et al. 2013; Wang et al. 2013).

The identification of candidate genes (regions) underlying QTLs for economically important traits is essential for marker-assisted selection (MAS) and map-based cloning (Arcade et al. 2004; Holland 2007). Candidate genes for some important traits have been identified by molecular mapping associated with genomic information and bioinformatics tools in many crops, including rice (Abe et al. 2012), maize (Wang et al. 2013), wheat (McIntyre et al. 2012), tomato (Chapman et al. 2012), and soybean (Peiffer et al. 2012; Chen et al. 2015). Many genes controlling lodging related traits, such as branch number (Finet and Jaillais 2012), root development (Puig et al. 2012) and lignin content (Bonawitz and Chapple 2010), and internode length and plant height (Yamaguchi 2008) have been identified and cloned in plants. In soybean, some genes controlling plant height (Zhang et al. 2015; Zhao et al. 2015; Zhou et al. 2015), number of nodes (Zhou et al. 2015), internode length (Zhao et al. 2015; Zhou et al. 2015), stem growth habit (Liu et al. 2010; Ping et al. 2014), and stem thickness (Zhao et al. 2015) have been identified. In addition, the integration of the whole genome sequence with the dense genetic marker map and annotation of the genome is available (http://www.phytozome.net/soybean) in soybean. Thus, identification of candidate genes responsible for quantitative traits by QTL mapping associated with genomic information and bioinformatics tools will be more efficient and reliable (Schmutz et al. 2010).

The objectives of this study were to (a) identify the main factors influencing lodging in soybean, (b) detect QTLs for lodging percentage (LP) and related traits (branch number (BN), internode length (IL), number of nodes (NN), plant height (PH), root length (RL), root fresh weight (RW), stem diameter (SD), stem strength (SS)) in multiple environments, and (c) dissect the genetic basis and correlations between lodging and related traits.

Materials and methods

Plant materials, field experiments, and trait measurements

The RIL population was developed by the single seed descent method from Zhongdou No. 29 (lodging-resistant cultivar) × Zhongdou No. 32 (lodging susceptible cultivar) cross and was bulk harvested at the F_6 generation (Wang 2008). The RIL population (165 lines) and their parents were planted on the farm of our institute (Oil Crops Research Institute of the Chinese Academy of Agricultural Sciences, Wuhan, China) in 2006 (E1), 2007 (E2), and 2008 (E3), using a randomized complete block design with three replications. Each plot contained three rows of 3.3 m long, with 0.4 m between rows and 0.1 m between individual plants.

Five plants from each plot were sampled and investigated for branch number, internode length, number of nodes, plant height, stem diameter, stem strength, root length, and root weight at podding stage. Internode length was calculated as follows: IL = plant height/number of nodes. Stem strength was measured using a prostrate tester made in Japan (DIK-7400, Daiki Rika Kogyo Co. Ltd., Tokyo). The prostrate tester was set perpendicularly to the plants at 20 cm height. When plants inclined to 30° from the vertical, pushing resistance was measured and estimated using the following formula: SS (gram per stem) = test value/40 × 1000 (Kashiwagi and Ishimaru 2004). At maturity stage, single plant with an angle of less than 30° between stem and horizontal was defined as lodging plant. Lodging percentage of each plot was calculated as follows: lodging percentage = number of the lodging plants/total plants of the plot (Qiu and Chang 2006).

Statistical analysis

Phenotypic data were analyzed using SAS version 9.1 (SAS 2004). PROC MIXED was used to calculate broad-sense heritability, and $h^2 = \sigma^2_{\mathrm{g}}/\sigma^2_{\mathrm{p}} = \sigma^2_{\mathrm{g}}/(\sigma^2_{\mathrm{g}} + \sigma^2_{\mathrm{e}}/r)$, where σ^2_{g} is genetic variance, σ^2_{p} is phenotypic variance, σ^2_{e} is the error variance, and r is the number of replications (Holland et al. 2003). The genetic correlation was calculated as $r\mathrm{G} = \mathrm{COV}_{\mathrm{G}xy}/(\sigma^2_{\mathrm{G}x} \times \sigma^2_{\mathrm{G}y})^{1/2}$, where $\mathrm{COV}_{\mathrm{G}xy}$, $\sigma^2_{\mathrm{G}x}$, and $\sigma^2_{\mathrm{G}y}$ are the genotypic covariance and variance of the pairwise traits, respectively (Holland 2006), and estimates of components of variance and covariance were obtained using the SAS procedure (SAS 2004; Shi et al. 2009). The significance of phenotypic and genetic correlation was determined using a t test of the correlation coefficients. Multiple linear regression analysis ($P < 0.05$) was performed to model the relationship between lodging percentage (dependent variable) and related traits (independent variables). The mean values of three environments were used in stepwise regression analysis of forward selection and backward elimination (SAS 2004; Nathans et al. 2012). Separate regression analyses ($P > 0.05$ for variable rejection) were performed with different sets of independent variables for (I) the entire eight lodging related traits and (II) except for plant height.

Molecular marker analysis and linkage map construction

Genomic DNA of RILs and parents was extracted from five bulked seedlings using CTAB method (Keim et al. 1988). The genotypes of the RILs were analyzed using simple sequence repeat (SSR) to enable the construction of a genetic linkage map. SSR primers (Song et al. 2004, 2010) were synthesized by Integrated DNA Technologies Inc. A total of 1147 SSR primer pairs (Song et al. 2004, 2010) were employed to screen polymorphism between two parents. Polymerase chain reaction (PCR) was conducted in 96-well microplates with a final volume of 20 μl. Each reaction included 50 ng of genomic DNA, 0.2 μm of each of the primers, 0.2 mm each of dNTPs, 2.0 mm of $MgCl_2$, and 0.2 U of Taq DNA polymerase. The PCR reaction was performed at 94 °C for 5 min, followed by 35 cycles of 94 °C for 30 s, 47 °C for 30 s, 72 °C for 45 s, with a final extension for 10 min at 72 °C. The PCR products were analyzed by electrophoresis in 6% polyacrylamide gels, and DNA fragments were visualized by silver staining (Bassam et al. 1991).

The genetic linkage map was constructed using Joinmap 3.0 (Van Ooijen and Voorrips 2001) with Kosambi mapping function (Kosambi 1944). Segregation distortion was performed by the chi-squared test ($P < 0.05$) with the JoinMap software under the “Locus Genotype Frequency” command. Parameters were set as default, i.e., LOD grouping thresholds greater than or equal to 2.0. Linkage groups were assigned according to Song et al. (2004) and the composite maps at the SoyBase website (http://www.Soybase.org).

Comparison of linkage map with physical map

Physical positions of SSR markers were obtained from SoyBase website (http://www.Soybase.org) and the BARCSOYSSR_01 soybean simple sequence repeat database (Song et al. 2010).

Markers without physical positions in SoyBase and BARCSOYSSR_01 database were in silico mapped on genome by using BLAST hits from SSR primer sequences against soybean genome. The blast results were screened for *e* values below 1.0, and size ranges between 50 and 400 bp (Kelleher et al. 2007). According to the positions on genome, the SSR markers on our linkage groups were mapped to the physical map using the BioMercator V3 software (Sosnowski et al. 2012).

QTL detection and meta-analysis

Composite interval mapping (Zeng 1994) incorporated into WinQTL cartographer 2.5 software (http://statgen.ncsu.edu/qtlcart/WQTLCart.htm) was used to detect QTLs. The mean values of three replications in each environment were used in QTL analysis, and the threshold of experiment-wise error rate was determined by permutation analysis with 1000 repetitions. LOD values corresponding to $P = 0.05$ were used to identify significant QTLs. QTLNetwork 2.0 (Yang et al. 2007, 2008) with composite interval mapping method was used to detect QTL × environment (ae) interaction effects. Significance level of genome scan for putative QTL detection, and QTL × environment interaction effects was set at 0.05.

To determine whether the QTLs mapped on the same region from different environments and traits represent a single locus (meta-QTL), algorithms for QTL meta-analysis according to the positions and confidence intervals of the QTLs were used to estimate the number and positions of the meta-QTL (Goffinet and Gerber 2000; Arcade et al. 2004; Chardon et al. 2004). This approach, using the *Akaike* information criterion (AIC), provided the basis to determine the number of meta-QTL that best fitted the results on a given linkage group. It also groups the QTLs into classes that correspond to the same QTL and provides a consensus estimation of QTL positions. The two-round strategy of QTL meta-analysis was performed according to Shi et al. (2009). The QTLs detected in different environments for the same trait were first integrated into consensus QTLs by using the BioMercator2.1 software (Arcade et al. 2004; Chardon et al. 2004). The overlapped consensus QTLs of different traits were integrated into overlapping QTLs in the second round of QTL meta-analysis. The software also provides a method for calculating 95% confidence intervals for the meta-QTL,

$$CI = \frac{3.92}{\sqrt{\sum_{i=1}^{i=k} \frac{1}{S_i^2}}},$$

where S_i^2 is the variance of position of the QTL$_i$ and k is the total number of QTL integrated into the meta-QTL (Arcade et al. 2004).

For the consensus QTLs, the QTL nomenclature corresponded to “q” (abbreviation of QTL), followed by the abbreviation of the trait (e.g., PH), the chromosome number, and the serial number. For the overlapping QTLs, the nomenclature corresponded to “oq” followed by the chromosome number and the serial number (Shi et al. 2009).

Identification of candidate gene

The candidate genes on the confidence intervals of consensus QTLs for branch number, plant height, root weight, and stem strength were analyzed according to genome positions of the SSR markers flanking the pleiotropic QTL regions associated lodging percentage and related traits (Zeng et al. 2006). The keywords of gene function (enzyme) and name were used to search for candidate genes in the genome annotations (http://www.phytozome.net/soybean). According to the positions of flanking markers, the candidate genes were mapped on our linkage map using the BioMercator2.1 software (Arcade et al. 2004; Chardon et al. 2004).

Result

Phenotypic variation and correlation among traits

The two parents (Zhongdou No. 29 and Zhongdou No. 32) differed significantly in the nine traits of all the three environments, except in root length. In the RIL population, all traits showed a continuous distribution and transgressive segregation (Table 1). The coefficients of variation of the RIL population for these traits ranged from 12.3 to 72.1% in three environments. Lodging percentage showed significant positive correlations with branch number, internode length, number of nodes, plant height, and significant negative correlations with root weight, stem diameter, and stem strength in three

Table 1 Mean values and ranges of lodging and related traits in the parents and the RIL population

Traits	E	Parents			RILs		
		F	M	*t* test	Mean	Range	CV (%)
LP (%)	E1	17.8	62.5	***	43.2	0.0–100.0	62.0
	E2	16.2	80.8	***	60.3	2.9–100.0	50.5
	E3	17.2	71.5	***	53.1	2.2–96.6	72.1
	Mean	17.1	71.6	***	52.2	3.8–98.9	50.9
BN	E1	1.3	3.7	***	2.9	1.0–4.4	21.1
	E2	1.2	4.2	***	2.4	0.9–4.9	30.1
	E3	1.3	4.1	***	2.3	0.7–4.8	41.2
	Mean	1.3	4.0	***	2.5	1.3–4.3	22.8
IL (cm)	E1	4.1	4.9	**	4.3	3.1–5.5	23.4
	E2	3.7	4.7	**	4.0	3.0–5.5	25.4
	E3	4.1	5.0	**	3.8	2.8–5.2	25.5
	Mean	4.0	4.9	***	4.0	3.1–5.4	20.2
NN	E1	11.8	14.2	**	13.8	10.3–15.7	20.3
	E2	13.2	15.1	*	14.3	11.5–17.5	22.8
	E3	11.9	14.1	**	13.7	10.2–16.0	22.6
	Mean	12.3	14.5	*	13.9	10.6–16.7	21.5
PH (cm)	E1	48.7	69.7	***	58.7	41.3–81.8	40.4
	E2	49.4	71.4	***	60.9	43.9–85.3	41.7
	E3	48.3	70.3	***	53.2	35.8–76.5	43.5
	Mean	48.8	70.5	***	57.6	43.2–74.8	37.1
RL (cm)	E1	19.7	22.4		22.2	17.8–27.9	12.3
	E2	20.8	24.7	*	22.9	17.7–29.5	15.9
	E3	18.9	22.3		23.6	18.1–28.7	12.6
	Mean	19.8	23.1	*	22.9	18.4–27.8	13.4
RW (g)	E1	3.1	5.1	***	3.1	1.6–5.4	23.7
	E2	3.1	4.7	***	3.5	1.7–6.2	26.3
	E3	3.3	4.9	***	4.2	2.1–7.0	21.7
	Mean	3.2	4.9	***	3.6	1.8–5.3	19.5
SD (mm)	E1	5.8	6.6	*	6.0	5.0–7.6	25.2
	E2	5.5	6.4	*	6.0	4.2–6.8	25.5
	E3	5.8	6.8	*	6.2	4.9–7.6	23.8
	Mean	5.7	6.6	**	6.1	5.0–7.2	24.7
SS (g/stem)	E1	124.3	304.2	***	197.0	46.3–350.0	29.4
	E2	153.7	327.0	***	202.5	47.5–375.0	37.3
	E3	176.8	340.6	***	260.5	72.5–442.5	36.0
	Mean	151.6	323.9	***	220.0	62.1–380.0	32.2

LP lodging percentage, *BN* branch number, *IL* internode length, *NN* number of nodes, *PH* plant height, *RL* root length, *RW* root weight, *SD* stem diameter, *SS* stem strength, *E* environment, *F* Zhongdou No. 29, *M* Zhongdou No. 32

*$0.01 < P < 0.05$; **$0.001 < P < 0.01$; ***$P < 0.001$

environments (Table 2). ANOVA analysis showed that genotype, environment, and the interaction of environment × genotype (E×G) had significant effects ($P < 0.05$) on the nine traits in the RIL population, except the interaction (E×G) of branch number, root length and root weight, and the

Table 2 Phenotypic (above the diagonal) and genetic (below the diagonal) correlations among the nine traits across three environments

	LP	BN	IL	NN	PH	RL	RW	SD	SS
LP		0.184**	0.309**	0.235**	0.493**	–0.005	–0.176**	–0.120*	–0.116*
BN	0.201*		0.121*	–0.031	0.076	–0.170*	–0.129**	–0.041	–0.128*
IL	0.428**	0.126		–0.139**	0.652**	–0.163*	0.004	0.053	–0.027
NN	0.332**	–0.031	–0.139		0.324**	0.112*	0.117*	–0.046	0.141**
PH	0.597**	0.076	0.820**	0.422**		–0.103*	0.074	0.008	0.053
RL	–0.007	–0.247**	–0.226**	0.121	–0.103		0.257**	0.003	0.265**
RW	–0.195*	–0.140	0.004	0.126	0.083	0.326**		0.431**	0.412**
SD	–0.269**	–0.043	0.055	–0.048	0.008	0.003	0.674**		0.306**
SS	–0.170*	–0.154*	–0.029	0.153	0.061	0.334**	0.700**	0.510**	

LP lodging percentage, *BN* branch number, *IL* internode length, *NN* number of nodes, *PH* plant height, *RL* root length, *RW* root weight, *SD* stem diameter, *SS* stem strength

*$0.01 < P < 0.05$; **$P < 0.01$

broad-sense heritability (h^2) of the nine traits ranged from 0.33 to 0.68 (Table 3).

Regression analysis

Two models were developed by stepwise regression analysis: model I: $\text{LP}\ (\%) = -75.7714 + 2.5262\ \text{PH} - 9.2017\ \text{RW} + 9.0941\ \text{BN} - 0.0712\ \text{SS}$, 62.09% of variation in LP was explained by plant height (37.04%), root weight (18.40%), branch number (5.12%), and stem strength (1.53%); model II: $\text{LP}\ (\%) = -200.9686 + 31.7378\ \text{IL} - 8.6270\ \text{RW} + 8.7913\ \text{NN} + 8.5027\ \text{BN} - 0.0759\ \text{SS}$, 60.31% of variation in lodging percentage was explained by internode length (31.24%), root weight (12.29%), number of nodes (10.70%), branch number (4.41%), and stem strength (1.67%). The two models were similar with the independent variables of plant height in model I instead of internode length and number of nodes in model II. According to the partial R^2, plant height and root weight, which explain more than 55% of the variation in lodging percentage, should be the key factors influencing lodging in soybean (Table 4).

Construction of the genetic linkage map and comparison with the physical map

The amplified products of 348 SSR primer pairs (30.3% of the 1147 primers) showed polymorphic band pattern between the two parents. Interestingly, one pair of primers (Satt168) generates two markers: Satt168a and Satt168b. Based on these SSR markers and a phenotypic marker of LS (leaflet shape), a linkage map containing 315 markers was constructed for 20 chromosomes, while 14 unlinked markers and 21 significantly distorted markers were excluded. The linkage map covered 1501.5 centiMorgan (cM), and the average distance between markers was 5.3 cM. The order of 78.7% markers is consistent with the composite maps at the SoyBase website (http://www.Soybase.org). Regions with inverted marker order and intrachromosomal

Table 3 Significance of ANOVA analysis and estimates of heritability for lodging percentage and related traits in soybean RIL population

Source	DF	LP	BN	IL	NN	PH	RL	RW	SD	SS
Genotype	164	***	***	***	***	***	***	***	***	***
Environment	2	***	***	***	***	***	***	***	***	***
E×G	328	*	ns	*	***	***	ns	ns	*	**
h^2		0.53	0.42	0.61	0.39	0.68	0.33	0.51	0.46	0.40

DF degrees of freedom, *h2* broad-sense heritability, *E× G* environment ×genotype, *LP* lodging percentage, *BN* branch number, *IL* internode length, *NN* number of nodes, *PH* plant height, *RL* root length, *RW* root weight, *SD* stem diameter, *SS* stem strength, *ns* not significant

*$0.01 < P < 0.05$; **$0.001 < P < 0.01$; ***$P < 0.001$

Table 4 Parameters and statistics of stepwise regression models for the relationship between lodging and related traits

Variable	Summary of stepwise selection			Summary of parameter estimates			
	Partial R^2	*F* value	*P* value	PE	SE	*t* Value	Pr > |t|
PH	0.3704	95.90	<.0001	2.5262	0.1775	14.23	<.0001
RW	0.1840	66.91	<.0001	–9.2017	2.7566	–3.34	0.0010
BN	0.0512	20.88	<.0001	9.0941	1.9769	4.60	<.0001
SS	0.0153	6.47	0.0119	–0.0712	0.0280	–2.54	0.0119
Intercept				–75.7714	10.7182	–7.07	<.0001
Model I: LP (%) = −75.7714 + 2.5262 PH − 9.2017 RW + 9.0941 BN − 0.0712 SS							
IL	0.3124	74.05	<.0001	31.7378	3.0884	10.28	<.0001
RW	0.1229	35.25	<.0001	–8.6270	2.8419	–3.04	0.0028
NN	0.1070	37.64	<.0001	8.7913	1.3027	6.75	<.0001
BN	0.0441	17.04	<.0001	8.5027	2.0408	4.17	<.0001
SS	0.0167	6.71	0.0105	–0.0759	0.0293	–2.59	0.0105
Intercept				–200.9686	21.0427	–9.55	<.0001
Model II: LP (%) = – 200.9686 + 31.7378 IL – 8.6270 RW + 8.7913 NN + 8.5027 BN – 0.0759 SS							

PE parameter estimate, *SE* standard error, *LP* lodging percentage, *BN* branch number, *IL* internode length, *NN* number of nodes, *PH* plant height, *RW* root weight, *SS* stem strength

rearrangements were observed on linkage map compared to the physical map.

QTL detection and meta-analysis

With the method of composite interval mapping (CIM), 36, 31, and 37 QTLs associated with the nine traits were identified in E1, E2, and E3, respectively. These QTLs were distributed on 13 chromosomes and explained 4.8–28.4% of the phenotypic variance. The majority of these QTLs were clustered on chromosomes 6, 8, 13, and 19; therefore, they were subjected to the first round of QTL meta-analysis trait by trait and resulted in 64 consensus QTLs (Online Resource 1, Fig. 1). A total of nine consensus QTLs for lodging percentage were identified in one to three environments, of which four and three were detected on chromosomes 13 and 19, respectively. For eight lodging-related traits, 2–11 consensus QTLs were detected in 1–3 environments (Online Resource 1, Fig. 1).

Most of the consensus QTLs for each trait overlapped with those for other traits. For example, five consensus QTLs were mapped on a small interval (27.8–43.1 cM) of chromosome 13 (Online Resource 1, Fig. 1). Therefore, the 64 consensus QTLs of different traits were subjected to the second round of QTL meta-analysis, which resulted in 53 overlapping consensus QTLs being integrated into 17 pleiotropic overlapping QTLs (Online Resource 1, Fig. 1). Among these 17 QTLs, 1 overlapping QTL, *oq.8-2*, was responsible for six traits (internode length, number of nodes, plant height, root weight, stem diameter, and stem strength) and was located at the small interval of 23.7–26.1 cM on chromosome 8; 2 overlapping QTLs (*oq.6-2* and *oq.13-2*) were responsible for five traits; 4 overlapping QTLs (*oq.6-3*, *oq.8-3*, *oq.19-2*, and *oq.19-3*) were responsible for four traits; 1 overlapping QTL, *oq.13-1*, was responsible for three traits; and 8 overlapping QTLs (*oq.1-1*, *oq.4-1*, *oq.4-2*, *oq.13-3*, *oq.13-4*, *oq.14-1*, *oq.14-3*, *oq.16-1*, and *oq.20-1*) were responsible for two traits. In addition, 11 overlapping QTLs originated from a single consensus QTL and were responsible for only one of the nine investigated traits.

Of the 17 pleiotropic overlapping QTLs, 8 associated with lodging percentage and related traits were mapped on 4 chromosomes. The overlapping QTLs, *oq.1-1* was responsible for lodging percentage and number of nodes; *oq.13-1* was responsible for lodging percentage, branch number, and root weight; *oq.13-2* was responsible for lodging percentage, internode length, number of nodes, plant height, and stem strength; *oq.13-3* and *oq.13-4* were both responsible for lodging percentage and plant height; *oq.16-1* was responsible for lodging percentage and root length; and *oq.19-2* and *oq.19-3* were both responsible for lodging percentage, branch number, root weight, and stem diameter (Online Resource 1, Fig. 1).

QTL × environment interaction effects

A total of 20 environment-sensitive QTLs were detected for the nine traits (Online Resource 2). For lodging percentage, *qLP-13-2* and *qLP-19-3* with negative interaction effects were detected in two environments (E2 and E3); *qLP-13-3* and *qLP-16-1* with negative interaction effects were detected in E1 and E2, respectively. For lodging-related traits, nine environment-sensitive QTLs were detected in two environments and seven environment-sensitive QTLs were detected in single environments (Online Resource 2).

Candidate genes underlying consensus QTL of lodging-related traits

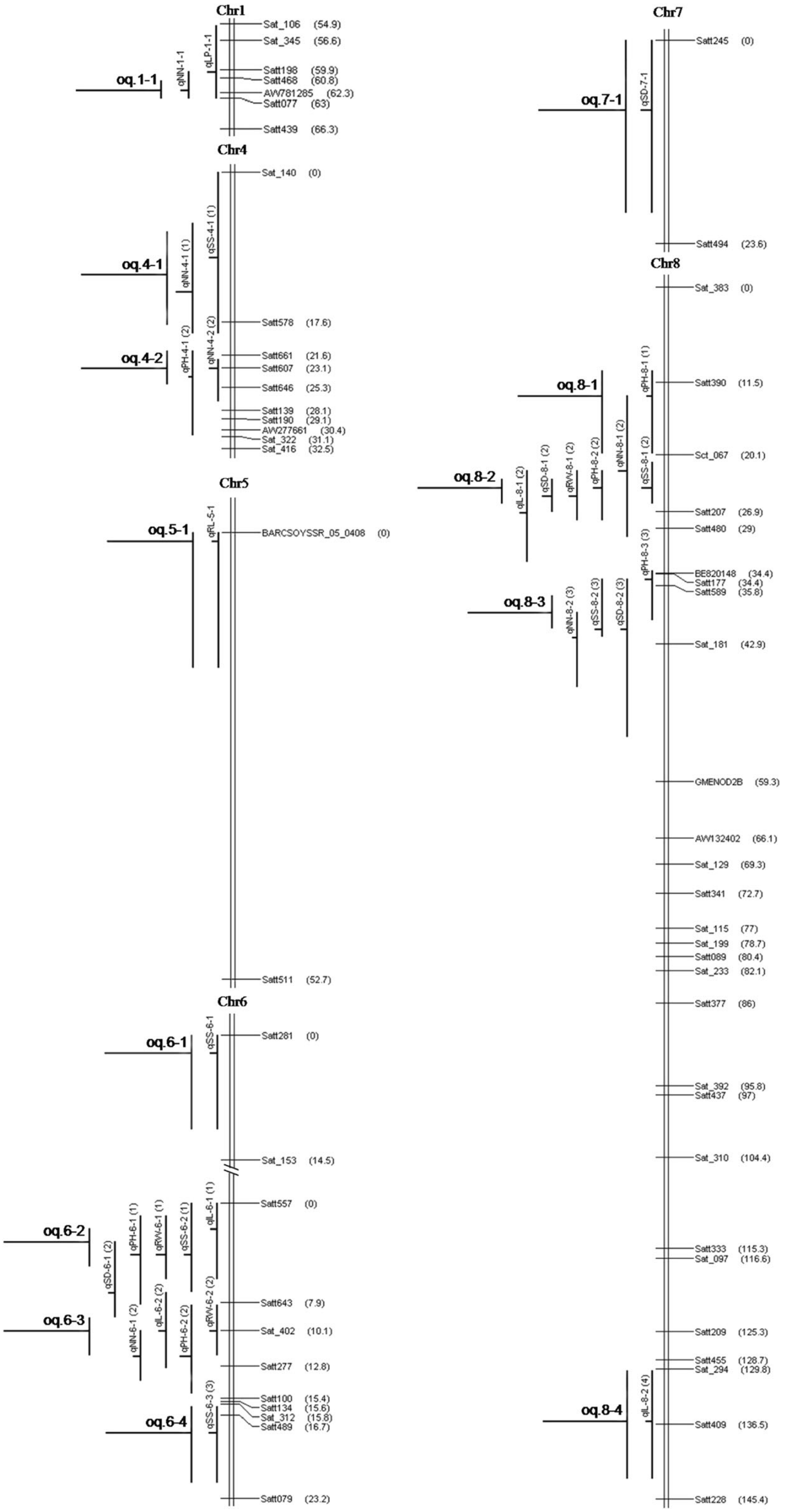
Using the annotated gene information available in the soybean database, seven candidate genes for lodging-related traits were identified on four pleiotropic QTLs (*oq.13-1*, *oq.13-2*, *oq.19-2*, and *oq.19-3*) regions (Fig. 1, Table 5). *Glyma13g29320* for auxin response factor related to lateral root formation and shoot branching was mapped on the pleiotropic QTL (*oq.13-1*) region associated with lodging percentage, branch number, and root weight. *Glyma13g35810* for R2R3-MYB transcription factor, which is related to lignin biosynthesis, was mapped on pleiotropic QTL (*oq.13-2*) region associated with lodging percentage and stem strength. *Glyma13g36360* for gibberellin 2-beta-dioxygenase related to internode elongation was mapped on the pleiotropic QTL (*oq.13-1*) region associated with lodging percentage, internode length, and plant height. *Glyma19g33680* for cytokinin synthase, which is related to root growth, was mapped on the pleiotropic QTL (*oq.19-2*) region associated with lodging percentage and root weight. *Glyma19g34370* and *Glyma19g34380* for AUX/IAA transcription factor related to elongation of root apex and axillary shoot branching were mapped on the pleiotropic QTL (*oq.19-2*) region associated with lodging percentage, branch number, and root weight; *Glyma19g35180* with the same function was mapped on another pleiotropic QTL (*oq.19-3*) region. Of the seven candidate genes, four have pleiotropic effects on branch number and root weight; one has pleiotropic effects on internode length and plant height.

Discussion

Considerable research into the genetic basis of lodging and related traits has been reported in rice (Kashiwagi and Ishimaru 2004; Islam et al. 2007; Kashiwagi et al. 2008; Tan et al. 2008), wheat (Keller et al. 1999; Foulkes et al. 2011), and maize (Farkhari et al. 2013; Landi et al. 2007). The genetic architecture of lodging in these crops was unambiguous; some key factors influencing lodging have been proposed and were used as important indexes of lodging resistance in breeding. Some studies contributed in mapping the QTLs of lodging, exploring the relationship between lodging and related traits in soybean (Lee et al. 1996; Orf et al. 1999; Wang et al. 2004; Guzman et al. 2007; Panthee et al. 2007; Kim and Diers 2009; Chen et al. 2011; Yamaguchi et al. 2014). However, the genetic architecture and key factors influencing lodging in soybean remain ambiguous. In the present study, the complexity of the genetic architecture of lodging was demonstrated by statistical analysis, QTL meta-analysis, candidate gene approach and illustrating the pleiotropy, variability, and synthesis of lodging QTLs.

In crops, QTLs or genes for economically important traits, such as yield, quality, and resistance to biotic and abiotic stress are usually clustered on genome (Xue et al. 2008; Tan et al. 2008; Liu et al. 2014). The pleiotropic QTLs may be caused by several tightly linked trait-specific genes (QTL hotspots) or a single gene that affected several traits (Clark et al. 2006; Tan et al. 2008; Xue et al. 2008). Previous studies have shown that QTL hotspots are widely distributed in genome and play important roles in species growth (Keurentjes et al. 2007; Michaelson et al. 2012; Neto et al. 2012). Moreover, evidence shows that pleiotropy of single gene is even more pervasive than previously imagined and occurs between traits that are not thought to be functionally related (Mackay et al. 2009). The pleiotropic gene of *prog1* with multiple effects in rice can increase the number of primary and secondary branches, grain number and yield, even lead to erect growth, was a key

Fig. 1 Overlapping QTL integrated from consensus QTL by the second round strategy of QTL meta-analysis. The *symbols* "┤" to the left of the linkage groups represent the positions of overlapping and consensus QTL for different traits. The length of the *vertical bar* in the "┤" *symbol* indicates the confidence interval of the QTL, and the position of the *horizontal bar* indicates the peak position of the QTL. Numbers in parentheses indicate the map coordinate in cM for linkage map ▶


Chr1
Sat_106 (54.9)
Sat_345 (56.6)
Satt198 (59.9)
Satt468 (60.8)
AW781285 (62.3)
Satt077 (63)
Satt439 (66.3)
oq.1-1
qNN-1-1
qLP-1-1
Chr4
Sat_140 (0)
Satt578 (17.6)
Satt661 (21.6)
Satt607 (23.1)
Satt646 (25.3)
Satt139 (28.1)
Satt190 (29.1)
AW277661 (30.4)
Sat_322 (31.1)
Sat_416 (32.5)
oq.4-1
oq.4-2
qNN-4-1 (1)
qSS-4-1 (1)
qPH-4-1 (2)
qNN-4-2 (2)
Chr5
BARCSOYSSR_05_0408 (0)
Satt511 (52.7)
oq.5-1
qRL-5-1
Chr6
Satt281 (0)
Sat_153 (14.5)
Satt557 (0)
Satt643 (7.9)
Sat_402 (10.1)
Satt277 (12.8)
Satt100 (15.4)
Satt134 (15.6)
Sat_312 (15.8)
Satt489 (16.7)
Satt079 (23.2)
oq.6-1
oq.6-2
oq.6-3
oq.6-4
qSS-6-1
qSD-6-1 (2)
qPH-6-1 (1)
qRW-6-1 (1)
qSS-6-2 (1)
qIL-6-1 (1)
qNN-6-1 (2)
qIL-6-2 (2)
qPH-6-2 (2)
qRW-6-2 (2)
qSS-6-3 (3)
Chr7
Satt245 (0)
Satt494 (23.6)
oq.7-1
qSD-7-1
Chr8
Sat_383 (0)
Satt390 (11.5)
Sct_067 (20.1)
Satt207 (26.9)
Satt480 (29)
BE820148 (34.4)
Satt177 (34.4)
Satt589 (35.8)
Sat_181 (42.9)
GMENOD2B (59.3)
AW132402 (66.1)
Sat_129 (69.3)
Satt341 (72.7)
Sat_115 (77)
Sat_199 (78.7)
Satt089 (80.4)
Sat_233 (82.1)
Satt377 (86)
Sat_392 (95.8)
Satt437 (97)
Sat_310 (104.4)
Satt333 (115.3)
Sat_097 (116.6)
Satt209 (125.3)
Satt455 (128.7)
Sat_294 (129.8)
Satt409 (136.5)
Satt228 (145.4)
oq.8-1
oq.8-2
oq.8-3
oq.8-4
qPH-8-1 (1)
qIL-8-1 (2)
qSD-8-1 (2)
qRW-8-1 (2)
qPH-8-2 (2)
qNN-8-1 (2)
qSS-8-1 (2)
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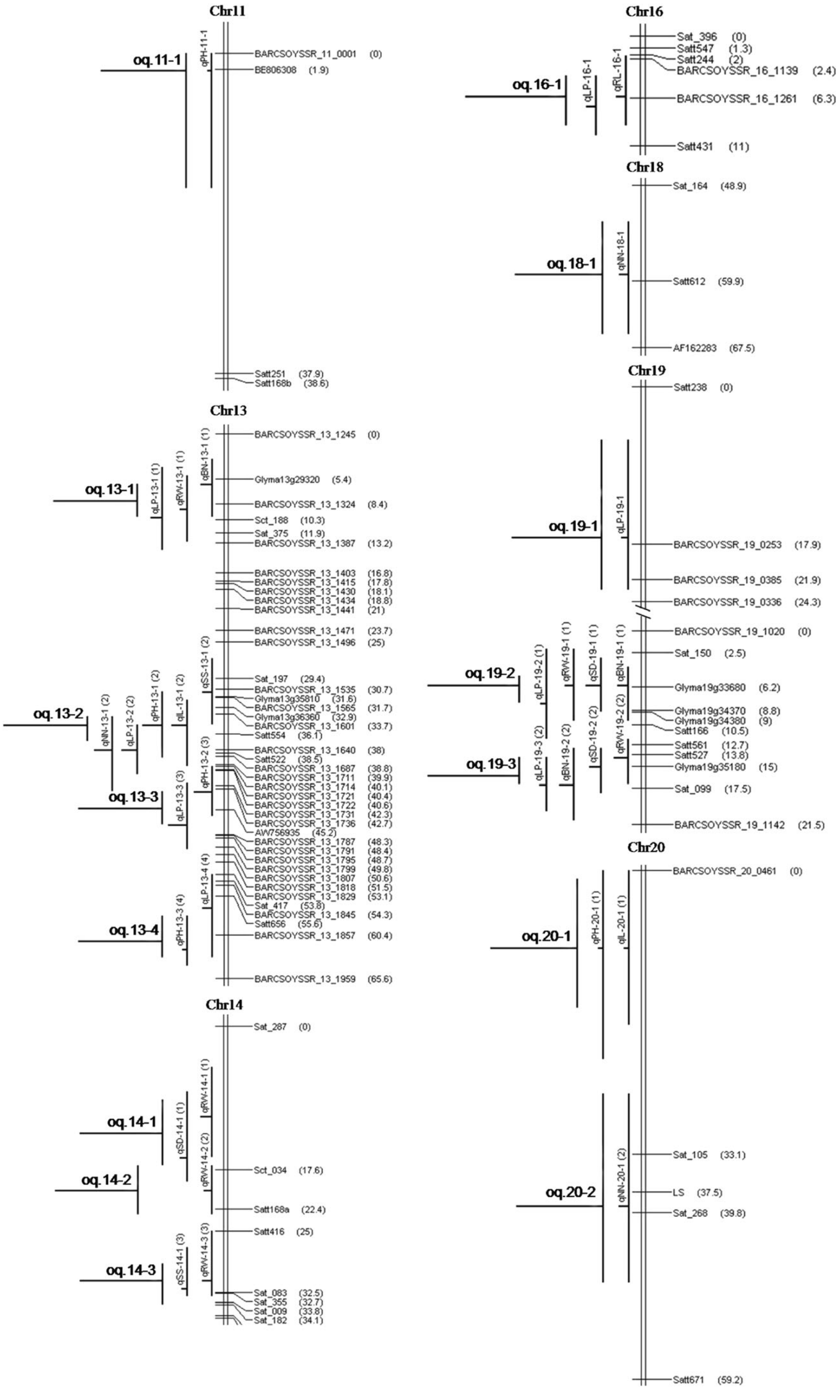
qIL-8-2 (4)



(continued)

gene controlling plant architecture and yield related traits (Li et al. 2006; Tan et al. 2008). In maize, the single gene *tb1* has pleiotropic effects on apical dominance, length of lateral branches, growth of blades on lateral branches, and development of the pedicillate spikelet in the female inflorescence (Hubbard et al. 2002; Clark et al. 2006). In present study, these colocalizations indicate that QTLs for lodging percentage are dependent on the QTLs of lodging-related traits; lodging is determined by the cumulative effect of many traits/processes of growth and development.

Table 5 Candidate genes for lodging related traits in soybean

Candidate gene	Tagged QTL	Function/enzyme	References
Glyma13g29320	*qBN-13-1*, *qRW-13-1*	Auxin response factor	Finet and Jaillais (2012)
Glyma13g35810	*qSS-13-1*	R2R3-MYB transcription factor	Bonawitz and Chapple (2010)
Glyma13g36360	*qPH-13-1*, *qIL-13-1*	Gibberellin 2-beta-dioxygenase	Yamaguchi (2008)
Glyma19g33680	*qRW-19-1*	Cytokinin synthase	Finet and Jaillais (2012)
Glyma19g34370	*qBN-19-1*, *qRW-19-1*	AUX/IAA transcription factor	Puig et al. (2012)
Glyma19g34380	*qBN-19-1*, *qRW-19-1*	AUX/IAA transcription factor	Puig et al. (2012)
Glyma19g35180	*qBN-19-2*, *qRW-19-2*	AUX/IAA transcription factor	Puig et al. (2012)

In present study, five consensus QTLs (*qLP-13-1*, *qLP-13-2*, *qLP-13-3*, *qLP-16-1*, and *qLP-19-3*) for lodging percentage were detected in multiple environments. The markers that are associated with these stable QTLs would be good candidates for MAS in soybean breeding. Evidence showed that the five consensus QTLs influenced lodging percentage resulted from the pleiotropic QTLs (*oq.13-1*, *oq.13-2*, *oq.13-3*, *oq.16-1*, and *oq.19-3*) for lodging-related traits. Thus, combination of the markers linked to lodging percentage and related traits will provide more effective approaches to developing lodging resistant cultivars with desired alleles in MAS. For example, pleiotropic QTL of *oq.13-1* is responsible for lodging percentage, branch number, and root weight, to detect the positive allele in MAS, the markers associated with the consensus QTLs for lodging percentage and the two related traits can be used together.

Lodging in soybean is a complex quantitative trait related to morphological/architectural traits and is highly affected by the environmental conditions (such as wind and rain) that can occur at different growth and development stages, and may not occur because of suitable environment and field management (Woods and Swearingin 1977; Mancuso and Caviness 1991; Board 2001); selection based on phenotype for lodging-resistant genotypes is very difficult and time consuming (Foulkes et al. 2011; Chen et al. 2011); thus, developing a suitable approach to predicting lodging is pivotal for the further improvement of lodging resistance in soybean. MAS has been proposed as a valuable tool in plant breeding and can be effectively used for the identification and pyramid of major genes and quantitative trait loci that exhibit large effects. However, complex traits, such as yield and lodging influenced by a large number of genes with individual small effect, will be difficult to deploy by MAS (Gu et al. 2014). Statistical models can predict gene-to-phenotype associations for complex traits and provide a way of overcoming the uncertainties associated with gene × environment interactions (Hammer et al. 2006). Therefore, the combination of MAS, statistical model, and phenotypic selection will be an effective approach to breed soybean with high lodging resistance.

In present study, the complexity of lodging was demonstrated by statistical analysis, QTL meta-analysis, and candidate gene approach and illustrating the pleiotropy, variability, and synthesis of lodging QTLs, which shed light on the understanding of the genetic architecture of lodging. The combination of lodging and related traits may be used as a selection index for lodging resistance with predicting lodging by model and assisted selection by markers in soybean breeding.

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Authors' contributions Chen H: designed the study, performed data analysis, and drafted the manuscript; Yang Z: performed phenotypic analysis and QTL mapping; Chen L and Wan Q: performed SSR analysis; Zhang C: analyzed QTL × environment interaction effects; Yuan S: bioinformatics analysis; Qiu D and Zhan Y: performed field experiments and traits measurement; Zhang X: isolated DNA; Chen S: prepared reagents; Shan Z: provided advice on the experimental design and reviewed the manuscript critically; Zhou X: designed the study. All the authors read and approved the final manuscript.

Compliance with ethical standards

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

Ethical standards The experiments comply with the current laws of China.

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